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Natália Matos de Menezes

FILOGEOGRAFIA DE CORAIS ESCLERACTÍNEOS NA COSTA DO BRASIL

PHYLOGEOGRAPHY OF BRAZILIAN SCLERACTINIAN CORALS

CAMPINAS

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Tese apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para a obtenção do Título de Doutora em Ecologia.

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Pois é pela mesma inquietação e nostalgia,
Que há no vasto clamor da maré cheia,
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E é porque as suas ondas desfeitas pela areia
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Por uma nova ilusão entontecida.
...”

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RESUMO

Recifes de corais são importantes ecossistemas para a biodiversidade marinha, entretanto, a sua história evolutiva tem sido pouco estudada. Os recifes brasileiros são considerados marginais devido a distância do centro de diversidade caribenho e às condições ambientais não ideais em que se desenvolvem. Estudos sugerem que a sua formação atual é recente uma vez que, no Último Máximo Glacial, o nível do mar teria descido 120 m e a plataforma continental onde ocorrem hoje estaria exposta. Hipóteses sobre a formação da sua diversidade atual incluem colonizações recentes a partir do Caribe ou dispersão a partir de refúgios climáticos em montanhas submersas próximas ao banco de Abrolhos. Neste trabalho, nós associamos abordagens filogeográficas à análises morfológicas e modelagens paleoclimáticas para estudar processos históricos responsáveis pela distribuição atual da diversidade de dois grupos de corais na costa do Brasil, o gênero *Siderastrea* e a espécie endêmica *Mussismilia braziliensis*. No primeiro capítulo, 'Phylogeography of the genus *Siderastrea* (Anthozoa, Scleractinia) in Southwest Atlantic: insights about the historical formation of coral biodiversity in marginal reefs', os resultados indicaram que as duas espécies do gênero encontradas no Brasil são muito similares às congêneres *S. radians* e *S. siderea* e que a endêmica *S. stellata* pode ser uma variação morfológica de *S. siderea,* o que mostrou a necessidade de uma revisão taxonômica do grupo. As análises intraespecíficas de diversidade genética, estrutura e demografia não corroboram as hipóteses de colonização recente e indicam que as espécies parecem ter mantido a sua amplitude latitudinal de ocorrência atual ao longo do tempo. No segundo capítulo, 'Paleoclimatic distribution and phylogeography of *Mussismilia braziliensis*, and endemic coral of Brazilian coast', tanto as análises filogeográficas quanto as simulações paleoclimáticas indicaram que a *M. braziliensis* também parece ter mantido a sua distribuição latitudinal ao longo das últimas variações no nível do mar. Os resultados para ambos os grupos sugerem que a costa do Brasil pode ter sido relativamente estável ambientalmente no tempo geológico em relação à outras regiões no Atlântico. Este trabalho traz importantes informações sobre os grupos estudados e sobre a biogeografia histórica dos atuais recifes de corais brasileiros.

ABSTRACT

Coral reefs are important ecosystems for marine biodiversity, however, their evolutionary history has been poorly studied. Brazilian coral reefs are considered marginal due to the distance from the Caribbean center of diversity and due to the suboptimal environmental conditions. The formation of their current reefs structures is very recent once the continental shelf where they occurs today were exposed in the Last Glacial Maximum. Some studies suggest colonization from the Caribe or dispersal from refuges in submerged mountain near the Abrolhos bank. Here, we associate phylogeographic approaches to morphological analysis and paleoclimatic modeling to study historical processes responsible for the current distribution of the diversity of two groups of Brazilian corals, the genus *Siderastrea* and the endemic species *Mussismilia braziliensis*. In the first chapter, entitled 'Phylogeography of the genus *Siderastrea* (Anthozoa, Scleractinia) in Southwest Atlantic: insights about the historical formation of coral biodiversity in marginal reefs', the results indicated that the two Brazilian species are strictly similar to the Caribbean congeners *S. radians* and *S. siderea* and that the endemic *S. stellata* seems to be a morphological variation of *S. siderea*, which showed the need for a taxonomic revision of the group. Genetic diversity, structure, and demography into both species do not corroborate the hypotheses of recent colonizations and indicate that the species have maintained their current latitudinal range of occurrence along geological time. In the second chapter, entitled 'Paleoclimatic distribution and phylogeography of *Mussismilia braziliensis*, an endemic coral of Brazilian reefs', both, phylogeographic analyzes and paleoclimatic simulations indicated that *M. braziliensis* also appears to have maintained its current latitudinal distribution over last sea level variation. The results for both studies suggest that the Brazilian coast remained environmentally stable when compared to other regions in the Atlantic along the geological time. This work presents important information on the general knowledge of the studied corals and on the historical biogeography of the current Brazilian coral reefs.

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INTRODUÇÃO GERAL

1. Recifes de corais e Biogeografia: distribuição da biodiversidade e regiões marginais

Os recifes de corais são ecossistemas marinhos costeiros mantidos pelo balanço entre processos de bioconstrução, por organismos capazes de depositar estruturas de carbonato de cálcio (principalmente corais escleractíneos zooxantelados), e processos de bioerosão, por organismos que escavam, raspam ou dissolvem estas estruturas (Glynn and Manzello 2015, Schmidt and Richter 2013). Este balanço confere grande complexidade e heterogeneidade estrutural aos recifes, o que lhes permite abrigar uma grande diversidade de organismos (Bozec et al. 2015). Embora ocupem uma área de cerca de 0.1 % de toda a área dos oceanos, possuem cerca de 34.3 % de toda a sua diversidade (Reaka-Kudla 1997), sendo conhecidos como um dos ecossistemas mais diversos do planeta (Connell et al. 1978).

Os recifes de corais são restritos a ambientes tropicais de águas rasas (Veron 1995) devido a dois motivos principais: a biomineralização da aragonita, principal tipo de carbonato de cálcio do esqueleto dos organismos bioconstrutores, diminui a baixas temperaturas (Muller-Parker and D'Elia 2015, Sheppard et al. 2009); e além disso, até 90% da nutrição dos corais escleractíneos vem da sua associação com algas dinoflageladas do gênero *Symbiodinium*, mais diversas e abundantes em regiões com alta incidência de luz (Muller-Parker and D'Elia 2015, Sheppard et al. 2009).

A diversidade desses ecossistemas não é homogeneamente distribuída na região tropical. O padrão mais evidente é conhecido como "bullseye", no qual a diversidade é alta em regiões conhecidas como centros de diversidade (e.g. Arquipélago Indo-Malaio no Oceano Indo-Pacífico e Caribe no Oceano Atlântico) e diminui em direção as zonas marginais (Veron 1995, Cowman et al. 2017). Entretanto, ao contrário do que é observado em ambientes terrestres, os centros de diversidade de recifes de corais não coincidem com seus centros de endemismo (Hughes et al. 2002). Regiões marginais possuem as maiores proporções de

espécies endêmicas ao passo que a maior parte das espécies dos centros de diversidade são amplamente distribuídas. A detecção deste padrão chamou atenção para a importância das regiões marginais para a diversidade (Bowen et al. 2013, 2016).

Recifes de corais marginais são aqueles que se estabelecem em condições ambientais não ideais ou em locais sujeitos a grandes flutuações ambientais (Kleypas, et al. 1999, Perry and Larcombe 2003). Em geral, ocorrem nas bordas da distribuição desses ecossistemas possuindo populações e diversidade genética menor em relação às centrais (Kawecki 2008, Nunes et al. 2011, Noreen et al. 2015, Grupstra et al. 2017). A condição marginal favorece a ocorrência de variações fenotípicas e genotípicas devido a seleção natural e deriva genética, gerando diversidade e processos de especiação (Rocha et al. 2008, Quenouille et al. 2011). De acordo com alguns autores, outros mecanismos como hibridação e introgressão também parecem se intensificar nas bordas da distribuição das espécies (Willis et al. 2006, Frade et al. 2010, Richards and Hobbs 2015).

A incorporação de uma perspectiva biogeográfica histórica para explicar a distribuição da diversidade em ambientes marinhos tropicais indica que muitas espécies surgiram em regiões marginais (Heck and McCoy 1978, Gaston 2003, Rocha et al. 2008, Hodge et al. 2013, Rocha et al. 2005); outras se mostraram amplamente distribuídas no passado e são atualmente restritas a essas regiões (Bellwood and Meyer 2009), ao passo que muitas colonizaram áreas marginais a partir de eventos de dispersão (Evans et al. 2016). Entretanto, a magnitude em que esses eventos ocorrem é desconhecida.

Uma revisão recente discute padrões temporais de origem da diversidade em ambientes recifais utilizando peixes recifais como organismo modelo, que é um dos grupos mais estudados. Em seu trabalho, os autores discutem a dificuldade em se construir estes padrões devido à escassez de dados sobre o assunto, principalmente em recifes de corais do Oceano Atlântico (Cowman et al. 2017). Ainda, o trabalho destaca que o investimento nessa área de estudo, o que inclui trabalhos com fósseis, estudos filogenéticos, tempos de divergência e estudos populacionais são essenciais para o avanço nessa área de conhecimento.

2. Recifes de corais Brasileiros

Os recifes de corais brasileiros se estendem de forma descontinua ao longo da costa brasileira por aproximadamente 3.000 Km, entre 0º50'S a 18º00'S. Apresentam variadas morfologias, tais como bancos recifais paralelos e adjacentes a costa, recifes em franja, *patch reefs*, um atol e uma formação endêmica de crescimento em forma de cogumelo designada 'chapeirão' (Leão et al. 2003). Eles são considerados marginais devido à sua distância do centro de diversidade Caribenho e devido às condições ambientais não ideais em que se desenvolvem (Leão et al. 2003, Dutra et al. 2006, Suggett et al. 2012). Dentre estas condições, destacam-se uma plataforma continental predominantemente curta, com pouca área para o estabelecimento de recifes, e uma alta turbidez da coluna d'água devido à grande quantidade de sedimentos oriundos do desague dos rios, além da erosão costeira e da ressuspensão desses sedimentos por ventos do sul (Leão and Dominguez 2000, Castro and Pires 2001, Leão et al. 2003, Segal et al. 2008). Recentemente, entretanto, os recifes brasileiros foram apontados como um centro de diversidade secundário para peixes no Oceâno Atlântico (Pinheiro et al. 2018).

A fauna coralínea dos recifes brasileiros é conhecida pela baixa diversidade de corais zooxantelados da ordem Scleractinea e pelo alto endemismo (Laborel 1969). No total, são registrados vinte e uma espécies, sendo que quatorze também ocorrem no Caribe e sete são endêmicas (Neves et al. 2006). Dentre as endêmicas, três possuem congêneres no Caribe, *Siderastrea stellata*, *Astrangia braziliensis* e *Meandrina braziliensis* e quatro, pertencem ao gênero *Mussismilia,* restrito à costa do Brasil. Outra característica peculiar dos corais zooxantelados brasileiros é a predominância do formato maciço hemisférico, característico das espécies de recifes antigos (Leão 1983, Leão and Kikuchi 2005), ao passo que os recifes atuais no caribe apresentam predominantemente espécies com formas ramificadas e porosas, representadas, por exemplo, pelos acroporídeos (Pandolfi and Jackson 2006).

Estudos indicam que a formação atual dos recifes brasileiros é bastante recente uma vez que provavelmente ocorreu após as últimas glaciações no Pleistoceno (Ludt and Rocha 2014). Pesquisadores discutem que variações climáticas neste período causaram regressões e transgressões no nível do mar em

todo o mundo, afetando principalmente ecossistemas costeiros como os recifes de corais (Budd 2000, Pellissier et al. 2014, Ludt e Rocha 2014). Estima-se que no último máximo glacial, há aproximadamente 21 mil anos, a linha de costa desceu cerca de 120 metros, deixando exposta a plataforma continental onde recifes ocorrem hoje, de forma que a colonização atual destes ambientes possivelmente ocorreu apenas depois deste evento.

No Brasil, estudos que buscam entender se as variações pleistocênicas no nível do mar podem ter interferido na distribuição atual da diversidade de corais são poucos. Alguns sugerem colonização recente de outros lugares do Oceano Atlântico, principalmente do Caribe, devido a semelhança entre suas faunas (Leão et al. 2003). Outros hipotetizam que a região de montanhas submersas de Vitória – Trindade, situada próximo ao Banco de Abrolhos de forma perpendicular à costa (Pinheiro et al. 2014), pode ter se mantido climaticamente estável em relação a outras regiões, servindo como áreas de refúgio para espécies recifais e permitindo a sua persistência ao longo do tempo (Leão 1983, Nunes et al. 2008). Estes refúgios seriam, então, fontes de colonização para os recifes atuais. Estudos moleculares recentes com peixes e com a espécie de coral *Mussismilia hispida* mostram evidências da ocorrência destes refúgios em montanhas submersas afastadas da costa (Pinheiro et al. 2017, Peluso et al. 2018). Entretanto, a formação da diversidade de corais na costa brasileira é um assunto que ainda precisa ser melhor explorado.

3. Ferramentas para estudar os padrões atuais e os processos históricos de formação da diversidade da fauna coralínea brasileira

Diferentes abordagens metodológicas tem sido utilizadas para estudar padrões atuais de diversidade e processos históricos responsáveis pela sua formação. Análises de variação morfológica constituem uma das primeiras e ainda hoje uma das principais ferramentas de descrição da diversidade tanto intra quanto interespecífica (Monteiro and Reis 1999, Budd and Stolarski 2011). Ao serem correlacionadas com variações ambientais ou com variações genéticas ao longo da sua distribuição, variações morfológicas podem ajudar a construir hipóteses sobre a formação da biodiversidade, bem como apoiar hipóteses já existentes (Todd 2008).

Para corais escleractíneos, a grande quantidade de traços morfológicos quantitativos tem exigido a utilização de técnicas multivariadas, estando as análises de componentes principais e as análises discriminantes entre as mais utilizadas para este grupo (Filatov et al. 2010, Menezes et al. 2013, Paz-García et al. 2015).

Na segunda metade do século XX, o avanço nos métodos de obtenção e análise de dados moleculares permitiu estudos cada vez mais aprofundados sobre a formação da diversidade. A Filogeografia surge neste contexto, na década de 80, como uma área da ciência que utiliza conceitos de Genética de Populações, Sistemática e Biogeografia para estudar os princípios e processos que determinam a distribuição geográfica de linhagens genealógicas (Avise et al. 1987). Os primeiros trabalhos filogeográficos foram baseados em dados de DNA mitocondrial e consistiam basicamente em sobrepor genealogias à distribuição das amostras avaliadas a fim de encontrar concordância entre as linhagens e sua localização no espaço (Martins and Domingues 2011). Nos últimos anos, a incorporação dos métodos de coalescência nas análises filogeográficas tem permitido inferir complexos cenários demográficos do passado a partir de informações genéticas atuais (Avise 2009). Um passo importante dessa área da ciência foi o fato de poder ser aplicado tanto a estudos macro quanto micro evolutivos, possibilitando avaliar processos evolutivos e biogeográficos em diferentes escalas (Avise 2009).

As metodologias da filogeografia tem sido amplamente aplicadas para testar hipóteses sobre a influência de eventos como variações no nível do mar, deriva dos continentes, correntes e outras barreiras semipermeáveis na história evolutiva dos organismos marinhos (Mirams et al. 2011, Baums et al. 2014, Ludt and Rocha 2014, Dohna et al. 2015). No Brasil, existe um grande esforço em ampliar os estudos filogeográficos com organismos marinhos, de forma que eles tem sido realizados com diversos organismos como peixes, esponjas, poliquetas, moluscos, crustáceos e cnidários (Rocha et al. 2008, Lazoski et al. 2011, Rua et al. 2011, Stampar et al. 2012, da Silva et al. 2016, Neves et al. 2016, Souza et al. 2016, Nunes et al. 2016, Pinheiro et al. 2017), entretanto, poucos foram realizados até o momento com corais escleractíneos (Neves et al. 2008, Nunes et al. 2011, Peluso et al. 2018).

Recentemente, modelagens de distribuição também tem sido utilizadas para entender a história biogeográfica da diversidade. Esta técnica identifica os fatores ambientais determinantes da distribuição espacial atual das espécies e projeta a sua possível distribuição no espaço e tempo, podendo inferir mudanças na distribuição de espécies e populações (Peterson et al. 2001). Em ambientes terrestres, essa metodologia foi utilizada para localizar áreas climaticamente estáveis no tempo geológico, que poderiam ser locais de refúgios em casos de flutuações climáticas (Carnaval et al. 2009, Peres et al. 2015); também foi utilizada para inferir eventos de expansão e retração de biomas e antigas conexões entre florestas tropicais (Carnaval and Moritz 2008, Leite et al. 2015, Sobral-Souza et al. 2015, Bartoleti et al. 2017). Em ambientes marinhos, modelagens de distribuição tem sido empregadas principalmente para prever a distribuição potencial atual ou futura das espécies (Tittensor et al. 2009, (Saupe et al. 2014); porém, poucos estudos tem realizado modelagens para o passado (Assis et al. 2014, Pellissier et al. 2014).

Dada a dificuldade e as incertezas associadas a estudos que tentam entender processos históricos de formação da diversidade, a utilização conjunta de diferentes metodologias tem sido recomendada por diversos autores (Knowles et al. 2007, Carnaval and Moritz 2008, Collevatti et al. 2015). De acordo com Gavin et al. (2014), que faz uma revisão sobre abordagens para estudar refúgios climáticos, a porcentagem de trabalhos que associam múltiplas linhas de evidência para inferir esses eventos passou de 17% entre 1999 e 2003 para 44% em 2013, tratando-se de uma tendência que vem crescendo com o passar dos anos. De acordo o autor, a combinação de diferentes técnicas pode auxiliar a inferir histórias evolutivas complexas, difíceis de serem analisadas apenas por uma perspectiva.

4. O ‘Complexo *Siderastrea* do Atlântico’ e a espécie *Mussismilia braziliensis*

Pertencentes a Ordem Scleractinia, o gênero *Siderastrea* e a espécie *Mussismilia braziliensis* são importantes componentes das comunidades coralíneas da costa do Brasil e possuem um papel considerável na construção da estrutura carbonática de alguns recifes. *Siderastrea* é o coral dominante na base dos recifes do Atol das Rocas, ao passo que *Mussismilia brasiliensis* é a principal construtora dos chapeirões dos bancos de Abrolhos (Leão et al. 2003). Ambos são corais

coloniais, maciços e de crescimento hemisférico ou incrustante, típico dos corais brasileiros.

O gênero *Siderastrea* de Blainville, 1830, compõe a Família Siderastreidae e se diferencia dos outros gêneros principalmente por seus septos seguirem um plano hexameral (Neves 2004) (Figura 2). Possui uma distribuição cosmopolita e é representado por quatro espécies: *S. savigniana*, que ocorre no Indo – Pacífico; *S. siderea* e *S. radians* que ocorrem em todo o Atlântico; e *S. stellata* que era considerada endêmica no Brasil, mas que foi registrada em 2017 no Golfo do México (Neves 2004, García et al. 2017). De ocorrência restrita a costa oeste do Panamá, *S. glynni*, era tida como uma quinta espécie, porém, foi recentemente sinonimizada a *S. siderea* (Glynn et al. 2016).

O grupo possui uma alta resistência a variações de temperatura, salinidade e sedimentação, além de ser encontrado em uma grande amplitude de profundidade (0 a 60 m) (Leão et al. 2003, Cordeiro et al. 2015). Informações sobre sua reprodução indicam que *S. siderea* é desovadora com fecundação externa enquanto as outras duas são incubadoras com fecundação interna (Neves and Da Silveira 2003). Estudos sobre variação e estruturação genética do gênero na costa do Brasil, realizados com marcadores moleculares, particularmente com isoenzimas e marcadores nucleares, apontam para uma capacidade de dispersão moderada para *S. radians* e *S. stellata* (Neves et al. 2008, Nunes et al. 2011).

A morfologia altamente variável dessas espécies tem causado grande dificuldade na sua taxonomia, motivo pelo qual são frequentemente denominados “Complexo *Siderastrea* do Atlântico” (Neves 2004, Menezes et al. 2013). Entretanto, estudos recentes tem indicado diferenças diagnósticas entre elas: *S. siderea* apresenta traços morfológicos com valores maiores e ciclos septais sempre completos, *S. radians* apresenta traços morfológicos menores e ciclos septais nunca completos ao passo que *S. stellata* apresenta morfologia intermediária, podendo ou não ter ciclos septais completos (Neves et al. 2010).

Dados moleculares, entretanto, apontam para informações contraditórias. Enquanto um estudo realizado com isoenzimas sugere que os grupos genéticos

encontrados no Brasil são as espécies *S. radians* e *S. stellata* (Neves et al. 2008), outro, com marcadores nucleares sugere que os grupos genéticos encontrados são as espécies *S. radians* e *S. siderea* (Nunes et al. 2011). Forsman et al. (2005), ao realizarem trabalhos filogenéticos com o gênero, aponta grande similaridade entre *S. radians* e *S. stellata*. Entretanto, no período do estudo, os autores não dispunham da informação da existência de pelo menos duas espécies de *Siderastrea* na costa do Brasil, de forma que o trabalho pode ter apresentado algum viés amostral e taxonômico. Apesar dos avanços, ainda é um grupo de taxonomia controversa, de forma que a realização de estudos sobre como processos históricos podem ter influenciado na sua diversidade atual pode auxiliar nas incongruências taxonômicas e melhorar o entendimento sobre o grupo.

A espécie *Mussismilia braziliensis* compõe o gênero *Mussismilia* Ortmann, 1890, que é endêmico da costa do Brasil (Figura 1 e 2). Dentre as quatro espécies do gênero, é a que possui a menor distribuição, ocorrendo entre o norte da Bahia e o norte do Espírito Santo, em aproximadamente 800 Km de costa. As outras espécies possuem ocorrência mais ampla: *Mussismilia hispida* é registrada do Maranhão a Santa Catarina; *Mussismilia harttii* ocorre do Rio Grande do Norte ao Espírito Santo; *Mussismilia leptophylla* é registrada no Maranhão e na costa da Bahia (Castro and Pires 2001, Leão et al. 2003, Amaral et al. 2007, Budd et al. 2012). Apesar de ser espacialmente restrita, *M. braziliensis* é uma das espécies mais abundantes em regiões como o Arquipélago de Abrolhos, sendo menos abundante em recifes ao norte da Bahia (Leão et al. 2003).

Estudos sobre a história de vida de *M. braziliensis* mostram que é uma espécie de reprodução anual que realiza fecundação externa – os gametas são liberados na água e a larva passa mais tempo sujeita a ação da movimentação da água (Pires et al. 1999). Devido a estas características reprodutivas, é esperado que possua uma ampla capacidade de dispersão, entretanto, trabalhos empíricos sobre o assunto não existem. Resultados de experimentos *in vitro* e o fato de possuírem pólipos relativamente grandes (~8mm) indicam que *M. braziliensis* pode resistir às condições de alta sedimentação característica da costa do Brasil (Loiola et al. 2013, Tenório 2016). Porém, devido a distribuição restrita, é considerada uma espécie vulnerável a impactos antrópicos e mudanças climáticas (Francini-Filho et al. 2008,

Garcia et al. 2013, Leão et al. 2016, Mazzei et al. 2016). O entendimento sobre a diversidade atual desta espécie e sobre como pode ter sido influenciada por processos históricos é de grande importancia para compreender o seu comportamento diante das atuais ameaças ambientais.

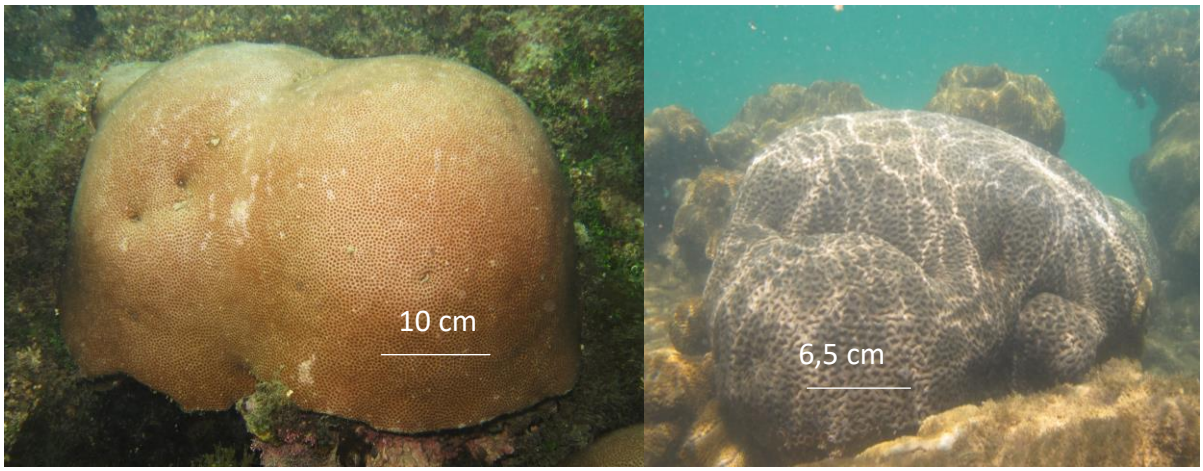

Figura 1. Imagens dos corais estudados. À esquerda, uma colônia de *Siderastrea* e, à direita, uma colônia de *Mussismilia braziliensis*. Fotos: Naália Menezes

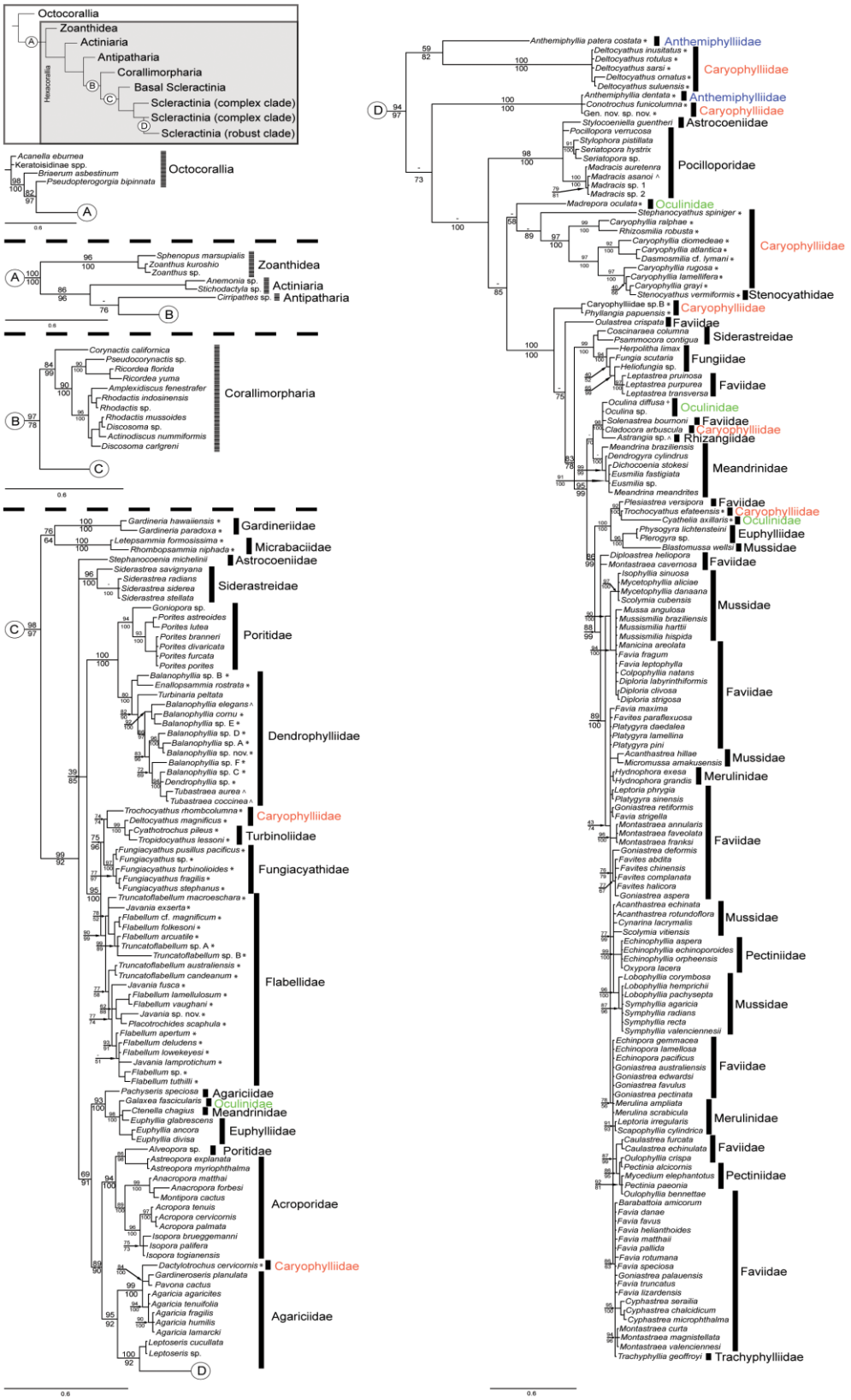

Figura 2. Filogenia da Ordem Scleractinia baseada no marcador molecular COI retirada de Kitahara et al. (2010).

OBJETIVOS DA TESE

O objetivo geral deste trabalho foi estudar os processos históricos responsáveis pela diversidade de corais escleractíneos da costa do Brasil. Para isso, utilizamos os grupos “Complexo *Siderastrea*” e a espécie endêmica *Mussismilia braziliensis*.

Os objetivos específicos da tese foram:

- Avaliar a variabilidade e estrutura genética do ‘Complexo *Siderastrea*’ e da espécie *Mussislimia braziliensis* na costa do Brasil
- Estimar relações filogenéticas e tempos de divergência entre os indivíduos dentro do ‘Complexo *Siderastrea*’ e da espécie *Mussislimia braziliensis* na costa do Brasil
- Inferir eventos demográficos para os grupos dentro do ‘Complexo *Siderastrea*’ e da espécie *Mussislimia braziliensis* na costa do Brasil
- Relacionar os resultados das análises baseadas em dados moleculares à resultados de análises morfológicas e de modelagem de nicho para os grupos de corais estudados

CAPÍTULO I

Phylogeography of the genus *Siderastrea* (Anthozoa, Scleractinia) in Southwest Atlantic: insights about the historical formation of coral biodiversity in marginal reefs

Abstract

Throughout the Atlantic Ocean, Brazilian coral reefs have a marginal and young formation that probably started to develop after the last sea level variations of the Pleistocene. Here we used a phylogeographic approach and morphological information to evaluate hypotheses about the influence of past events on the current distribution of scleractinian biodiversity in Brazilian reefs using the genus *Siderastrea*, a widely distributed group throughout the Atlantic Ocean. The phylogenetic results indicated that the two species found on the Brazilian coast are very similar to the Caribbean congeners *S. radians* and *S. siderea*, suggesting the need of broad taxonomical revision of the group. Genetic diversity, structure and demography in both species did not show evidence of recent colonization from the Caribbean or from possible Pleistocene refugia in submerged seamounts near Abrolhos bank, which indicated that the species of *Siderastrea* may have maintained their current latitudinal amplitude of occurrence since the Pleistocene period. Our data also corroborate hypothesis about the presence of phylogeographic barriers along the Brazilian coast. This study is important for understanding the historical biogeographic process responsible for assembling the current marginal scleractinian biodiversity of Brazilian reefs.

Introduction

Corals of the Order Scleractinia are keystone groups of coral reefs due to their role in building one of the most diverse and productive ocean ecosystems (Moberg and Folke 1999, Knowlton 2001, McClanahan 2003). Centers of scleractinian diversity, such as the Coral Triangle in the Indo-Pacific Ocean and Caribbean reefs in the Atlantic Ocean, have a well-known ecological relevance for marine biodiversity, acting as sources for colonization of other regions and improving their resilience capacity (Myers et al. 2000, Hughes et al. 2002, Roberts et al. 2002, Selig et al. 2014). The marginal areas of these corals' distribution range, however, have their importance for biodiversity that has only recently been evidenced. Several works indicate that marginal regions such as the Hawaiian Archipelago (Waldrop et al. 2016) and the Eastern Tropical Pacific (Hellberg et al. 2016), known for relative low diversity and high endemism, can act as biodiversity sources, exporting genetic diversity and morphological innovations (Budd and Pandolfi 2010, Hodge et al. 2011, Bowen et al. 2013, 2016). However, most studies with corals are still focused on Indo-Pacific Ocean areas, while marginal reefs in the Atlantic Ocean are still less studied (Rocha et al. 2008, Nunes et al. 2011, Pinheiro et al. 2018).

Marginal coral reefs are known for their sub-optimal ecological conditions for most organisms and high environmental fluctuations (Kleypas, et al. 1999). They generally occur at the edges of these ecosystems' distribution, with populations and genetic diversity lower than the central ones (Kawecki 2008) Nunes et al., 2011, Noreen et al. 2015, Grupstra et al. 2017). The marginal conditions favor genetic and phenotypic variations due to natural selection and genetic drift, which may lead to diversification processes (Kawecki 2008, Nunes et al. 2011, Noreen et al. 2015, Grupstra et al. 2017). Other important mechanisms, such as hybridization and/or introgression, are also common at the edges of species ranges (Willis et al. 2006, Frade et al. 2010, Richards and Hobbs 2015).

In the Atlantic Ocean, Brazilian coral reefs are considered marginal due to their distance from the Caribbean center of diversity and their turbid waters, unsuitable for coral growth (Leão et al. 2003, Suggett et al. 2012). They are discontinuously distributed along ~3000 km of the coast and are subject to different levels of sediment discharge from rivers/coastal erosion and re-suspension from

prevailing southerly winds (Leão and Dominguez 2000, Castro and Pires 2001, Leão et al. 2003, Segal et al. 2008).

Studies indicate that the formation of the current reefs' structures is very recent, since the sea level dropped about 120 m during the Last Glacial Maximum (~21 Ka), when the present-day continental shelf was exposed (Ludt and Rocha 2015). The origin of their diversity, however, is little known. Some studies suggest colonization from other regions of the Atlantic Ocean, mainly from the Caribbean, because of the similarity between their fauna (Leão et al. 2003). Other authors hypothesize that the region of submerged mountain Vitória - Trindade, located perpendicular to the coast and near to the Abrolhos Bank (Pinheiro et al. 2014), may have remained climatically stable, serving as a refugium for reef species and allowing their persistence over time (Leão 1983, Pinheiro et al. 2017); thus, these refugia would be sources of colonization for the present reefs. Recently, evidence supporting both hypotheses was observed for the coral *Mussimilia hispida* (Peluso et al. 2018). However, this topic is still rarely explored for Brazilian scleractinian corals, if we consider the complexity of evolutionary studies and that species could respond in different ways to environmental events over time.

Siderastrea is an important genus of reef-building coral on the Brazilian coast, occupying different environments and extreme conditions of temperature, sedimentation and ocean acidification (Laborel 1969, Lirman et al. 2002, Castillo et al. 2014, Horvath et al. 2016). The genus exhibits fossil records dating from the Cretaceous (~130 Ma) in places such as the Czech Republic (Eliásová 1997), Germany (Löser 1998), Jamaica (Mitchell 2002), Mexico (Baron-Szabo et al. 2006), Oman (Metwally 1996), Slovenia (Turnsek 1997), Texas, USA (Wells 1933) and Sergipe, Brazil (Mascarenhas 2004). However, it is composed of few living species. *Siderastrea savignyana* occurs throughout the Indo – Pacific; *Siderastrea siderea* occurs in the eastern Pacific and the whole Atlantic Ocean (Glynn et al. 2016), *Siderastrea radians* has an Amphi-Atlantic distribution (Neves et al. 2008) and *Siderastrea stellata,* usually considered endemic to South Atlantic, was recently reported in the Gulf of Mexico (Neves et al. 2010, García et al. 2017).

The Atlantic siderastreids have a long history of taxonomical controversies due to the uncertain boundaries among species and their phylogenetic proximity, and

they are commonly referred to as the 'Atlantic *Siderastrea* Complex' (Werner 1996, Neves 2004). Although several studies have ratified their specific status (Neves and Da Silveira 2003, Neves et al. 2008, 2010), some issues are still unclear. While an extensive isoenzymatic study along the coast shows that the two genetic groups found in Brazil are morphologically characterized as *S. stellata* and *S. radians* (Neves et al. 2008), a comparative analysis using intronic regions shows that Brazilian siderastreids are very similar to *S. radians* and *S. siderea* (Nunes et al. 2011). Thus, questions as whether Brazilian siderastreids are composed of multiple ecomorphs of two phenotypically plastic species (*S. radians* and *S. siderea)* found in the Caribbean, or if *S. stellata* is a third species, remain uncertain. The absence of studies about the historical diversification of *Siderastrea* lineages in a marginal region such as the Brazilian coast could be an aggravating factor for these controversies.

In this work, we investigated historical biogeographic processes that could have influenced the diversification and current diversity distribution of the 'Atlantic *Siderastrea* complex' in the marginal Brazilian coral reefs through a phylogeographic approach. Our specific objectives were (1) to identify the siderastreid species occurring on the Brazilian coast and (2) to test a biogeographic hypothesis that could explain the genetic diversity observed in Brazilian siderastreids. We tested the following hypotheses: (i) recent colonization from the Caribbean; (ii) recent colonization from Pleistocene refugia in the submarine mountain chain near Abrolhos Bank; (iii) colonization from both cited regions; (iv) absence of change in the latitudinal amplitude of occurrence over time. If (i) is true, we expect to observe ancient lineages and higher genetic diversity in populations closer to the Caribbean; if (ii) is true, we would also detect ancient lineages, but higher genetic diversity in populations near the Abrolhos region; if (iii) is true, we expect to find two centers of diversity; and if (iv) is true, we would detect absence of genetic structure. Additionally, we expect to find evidence of recent demographic expansion if (i), (ii) and (iii) are true and no signs of recent demographic fluctuations if (iv) is the correct hypothesis.

To address these objectives, we sequenced three nuclear DNA regions of *Siderastrea* samples, inferred their phylogenetic relationships and lineage divergence times, and estimated the populations' genetic diversity, structure and demographic patterns. We compared these genetic data to morphological information and, based

on our results, we discussed the possible biogeographic events that influenced the diversification and structure of the 'Atlantic *Siderastrea* Complex' in the Southwest Atlantic.

Material and Methods

Study sites, sample collection and identification

We sampled fragments of *Siderastrea* (~5 cm) from 16 sites along the Brazilian coast (Table 1). We chose colonies that were at least 2 m apart and we used a hammer and chisel to remove them, taking care to minimize the damage to the whole colony. We scraped the fresh tissue off the living surface, put it in vials of 1.5 ml containing anhydrous alcohol or guanidine thiocyanate solution (4 M guanidine thiocyanate, 0.1% N-lauroyl sarcosin sodium, 10 mM Tris pH8, 0.1 M 2-mercaptoethanol), and stored it at freezing temperature until extraction. The skeletons were labeled and bleached overnight in a solution of 2% sodium hypochlorite, rinsed and air-dried for morphotype assignment, since field identification was infeasible (Neves et al. 2010). Skeleton fragments of Abrolhos Region, Tinharé – Boipeba Archipelago and Atol das Rocas were not collected because of logistical issues.

The taxonomic identification was primarily based on morphological diagnosis (Neves 2004, 2010); however, since we did not have the skeletons of all individuals, we also used an ITS marker as a species 'barcode' region to identify them (Forsman et al. 2005, Fukami et al. 2004). Although some authors question the power of this marker to infer relationships at species and lower levels in scleractinian studies (Vollmer and Palumbi 2004), Forsman et al. (2005) showed that it has appropriate resolution and phylogenetic signal for *Siderastrea* and *Porites*. All individuals were sampled under permits granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, permit nos. 39090, 50521, 51433). The specimens were labeled and deposited in the Cnidaria Collection at the 'Museu de Zoologia da Universidade Federal da Bahia' (UFBA) as follows: Titanzinho/CE – UFBA1163; P. Búzios/RN – UFBA1167; S.J. Milagres/AL – UFBA1768; Coruripe/AL – UFBA1160; Itacimirim/BA – UFBA1164; B. T. Santos/BA UFBA1165, 1166; Caramuanas/BA – UFBA1159, 1169; P. Seguro/BA – UFBA1161; Cabo Frio/RJ – UFBA1162.

DNA extraction, amplification and sequencing

The genomic DNA was extracted using a phenol protocol described by Nunes et al. (2009). Three nuclear markers were used: the Internal Transcribed Subunit region (ITS), the carbonic anhydrase region (CAG) and the Signal Recognition Particle 54-kDa region (SRP54). ITS was amplified using primers ITS-1 and ITS-4 (White et al. 1990), and thermal profile had initial denaturation step at 96°C for 2 min; 35 cycles at 95°C for 10 s, 52°C for 30 s and 70°C for 4 min; and extension at 70°C for 2 min. CAG was amplified using primers 3-550 F and 3-550 R (Macdonald et al. 2011), and thermal profile had initial denaturation step at 95°C for 4 min; 35 cycles at 95°C for 45 s, 62°C for 45 s and 72°C for 2 min; and extension at 72°C for 10 min. SRP54 was amplified with primers SRP54Madfor and SRP54Madrev2 (Frade et al. 2010), and thermal profile had initial denaturation step at 94°C for 2 min; 35 cycles at 94°C 2min, 52°C for 30 s and 72°C for 1 min; and extension at 72°C for 2 min. All PCR reactions were carried out with a total volume of 25µl with 10 ng of genomic DNA, 3.0 mM $MgCl_2$, 1X of taq buffer, 0.4 mM of dNTP, 0.16 µM of each primer, 1U of Taq DNA polymerase and milli-q water.

The amplicons were analyzed in a Perkin-Elmer Prism 377 capillary sequencer. Sequences were aligned using the MAFFT algorithm under the default strategy (Katoh and Standley 2013), which has been shown to outperform when indels are plentiful, and manually inspected and edited in MEGA 6.0 (Tamura et al. 2013). Heterozygous sites were first coded according to IUPAC ambiguity codes, and the phased haplotypes were estimated using a Bayesian method employed in PHASE (Stephens and Donnelly 2003) based on the input files prepared with Dnasp v. 5.0 (Librado and Rozas 2006). The gametic phases were inferred with a minimum posterior probability of 0.9, usually recommended to reduce the number of unsolved haplotypes with false positives (Garrick et al. 2010).

Phylogenetic inference and divergence times

We constructed independent Bayesian gene trees using BEAST v.1.7.4. (Drummond et al. 2012b). The best fit nucleotide substitution models previously selected by AIC criterion in MEGA 6.0 (Tamura et al. 2013) were JC for ITS and TN93 and CAG for SRP54. Sequences other genera available on GenBank

(https://www.ncbi.nlm.nih.gov/genbank/) were used as outgroups. The outgroups were chosed based on availability in the data bases and phylogenetic proximity with *Siderastrea* (Figure x). *Coscinaraea columna* (AB441406.1) *and Psammocora contigua* (AY722784.1) were used to root the ITS tree; *Acropora austera* (HQ441841.1), *A. millepora* (KC493137.1) and *Styllopora pistilata* (HM748807.1) were used to root the CAG tree; and *Madracis decactis* (HQ379122.1), *M. formosa* (HQ379131.1) and *Pocillopora* sp. (EU006863.1) were used to root the SRP54 tree. We inferred parameters from a run of 200 million steps, with trees sampled every 10,000 steps. After checking the highly effective sample sizes (ESS>200) in Tracer 1.5 (Rambaut and Drummond 2009), the first 20% of trees were discarded as burn-in in TreeAnnotator. The resulting maximum clade credibility (MCC) trees were drawn in Figtree 1.4.2 (Rambaut 2009).

We also inferred a concatenate time-calibrated phylogenetic hypothesis in BEAST v.1.7.4 using fossil record information on *S. siderea* and *S. radians*, which first appeared in the Dominican Republic around 15.7 Ma bp and 7.7 Ma bp, respectively (Johnson et al. 2008). We used an initial mean mutation rate of 0.004 substitutions/Mya, previously provided by Savard et al. (1993) for ITS, considering a lognormal relaxed clock and using only the individuals with the three nuclear regions sequenced. We specified unlinked substitution models, unlinked clock models and linked tree for the three markers. The analysis was run for 300 million generations, with a tree-sampling frequency of 10,000. We checked the convergence and effective sample sizes (ESS>200) in Tracer (Rambaut et al. 2009) and discarded the first 20% trees. We used Figtree 1.4.2 to draw the resulting MCC tree.

Haplotype networks, genetic diversity and population structure

We constructed haplotype networks in PopART v.1.7 (Leigh & Bryant, 2015), using the Median-joining algorithm (Bandelt et al. 1999). Because of the presence of *indels*, we previously edited the matrices performing a simple coding method (Simmons and Ochoterena 2000), which counts contiguous gaps as a fifth base change, implemented in SeqState 1.4.1 (Müller 2006). Molecular diversity indices, haplotype frequencies and pairwise differentiations among sample sites (Φ_{ST}) were calculated using Arlequin v. 3.5 (Excoffier & Lischer, 2010). Bayesian Analyses of Population Structure were also conducted for all datasets using BAPS v. 6.0

(Corander et al. 2008). We performed ten runs to estimate the most probable number of genetic groups in our data (k) in a range between 1 and 20.

Demographic analysis

We checked for neutrality and inferred historical demographic processes using Tajima's D (Tajima 1989), Fu's Fs (Fu 1997) tests and mismatch distribution analyses (Harpeding 1994) for each population and each species in Arlequin v. 3.5. To estimate possible changes in the population size (Ne) through time, we applied Extended Bayesian Skyline Plot (EBSP) analyses with all markers together and each locus separately using Beast v. 1.7.4 (Drummond and Rambaut 2007). We unlinked substitution rates, clock and tree models and specified a linear model of population size. Runs of 300 million interactions were conducted, with samples taken every 10000 generations. The first 20% samples were discarded as burn-in. Tracer v1.5 was used to check the quality of the parameters.

Morphometric analysis

After identification, we applied an exploratory analysis for morphological variation. We used a stereomicroscope supplied with a calibrated eyepiece to measure six characters involved in the description of *Siderastrea* (Laborel 1969, Budd 1990, Neves 2004): corallite diameter (corD), columellar diameter (colD), septal number (sepN), thecal thickness (tecThick), columellar depth (depth), and the average distance between adjacent sampled calices (corDist) (Neves 2004, Menezes et al. 2013). Only mature corallites ('old polyps' sensu Soong and Lang 1992) with at least the third cycle of the septa fully formed were examined. For each fragment, three corallites were selected for measurements and statistical analyses were based on the average of the three corallites. We performed a Principal Component Analysis (PCA). Data were standardized to log (2) to fulfill PCA assumptions. The Kolmogorov-Smirnov test showed normal distribution for data. Descriptive analyses were also carried out with mean, standard deviation and amplitude of measures from corallites used (See Results). We used the vegan (Oksanen et al. 2012) and ggplot2 (Wickham 2009) packages in R environment and Excel 2010 (Microsoft©) for the analyses. We used samples only from places that we could keep the skeletons: Fortaleza (n=6), P. Búzios (n=5), S. J. Milagres (n=6), Coruripe (n=5), Itacimirim

(n=8), BTS (n=8), Caramuanas (n=8), P. Seguro (n=8), Cabo Frio (n=8). We also included information on *S. siderea* from other studies to compare with our results (Neves 2004). Only samples from Fortaleza, P. Búzios, S.J.Milagres, Coruripe and Cabo Frio had correspondence with genetic data. For other places, we haphazardly chose the colonies for analysis.

Table 1. Localities, latitude and longitud, number of field sampling number of individuals sampled in field and database, number of individuals sequenced for each marker (ITS, CAG, SRP54) and number of individuals used in the morphometric analysis.

Localities	Latitude	Longitude	Nº field samples	Nº ind. ITS	Nº ind. CAG	Nº ind. SRP54	Nº ind. Morfometry
1-Panamá			21	21	-	-	1 (Neves 2004)
2-Titanzinho, CE	-3,707671	-38,46795	10	6	2	-	6
3-A. Rocas	-3,866349	-33,817222	30	8	4	10	-
4-P. Búzios, RN	-6,008056	-35,10583333	10	5	5	5	5
5-Pernambuco	-8,445833	-34,904166	3	3	-	-	-
6-S.J. Milagres, AL	-9,274489	-35,366172	10	2	4	5	6
7-Coruripe, AL	-10,16036	-36,134274	10	5	-	4	5
8-Itacimirim, BA	-12,60947	-38,021794	30	8	5	8	8
9-B.T.Santos, BA	-12,79761	-38,57143263	30	5	-	8	8
10-Caramuanas, BA	-13,13309	-38,736693	30	7	5	8	8
11-T. Boipeba, BA	-13,48917	-38,90361111	40	9	5	5	-
12-P. Seguro, BA	-13,67	-38,89416667	30	7	4	8	8
13-P. Leste, BA	-16,3329	-39,006936	30	5	4	7	-
14-P. Lixa, BA	-16,64876	-39,093364	30	5	5	5	-
15-P. Sul, BA	-17,68398	-38,96529374	30	4	-	5	-
16-P. Abrolhos, BA	-17,77615	-39,05079753	30	6	5	7	-
17-C. Frio, RJ	-17,96361	-38,70777778	10	8	5	7	8
Total			384	114	54	92	66

Results

Genetic diversity and sequence features

The ITS, CAG and SRP54 sequences obtained measured 573, 227 and 233 bp, respectively. ITS and SRP54 datasets exhibited high haplotype and nucleotide diversities, with several gaps and 79 and 43 polymorphic sites, respectively; CAG was much less variable, with 12 polymorphic sites and no gaps (Table 2). The three markers showed ambiguous peaks and, after the haplotype reconstruction in PHASE and the removal of sequences with posterior probability

lower than 0.9, we obtained 114, 92 and 53 solved sequences for ITS, SRP54 and CAG respectively.

Phylogenetic inferences and divergence times

Bayesian phylogenetic inferences presented different results for the three markers (Figure 1, 2 and 3). The ITS tree showed two well-marked groups, which were highly similar to the species identified as *S. siderea* and *S. radians* by previous studies (Forsman et al. 2005). Thus, we adopted this species' nomenclature to refer to these two groups throughout the paper. These lineages' divergence presents some correspondence with the clusters indicated by BAPS (see next section), represented by different colors in Figure 1: while the red cluster is monophyletic, blue and beige clusters exhibit paraphyly. The CAG tree did not present groups with strong support, and the SRP54 tree showed two deeply divergent groups. When we compared the three gene trees, we observed no concordant monophyly among the groups, although some resemblance in topology should be observed between ITS and CAG trees (Figure 1 and 2).

The time-calibrated tree using all markers showed that *Siderastrea* diverged from the outgroup at ~127.6 Ma [95% highest posterior density (HPD) = 27.1-311.8 Ma]; and the divergence between *S. radians* and *S. siderea* occurred at ~29.02 Ma (95% HPD = 15.6-59.8 Ma). More recent diversifications were also observed, but were not considered because of the low posterior probability (Figure 4).

Haplotype networks and population structure

Each haplotype network was constructed using samples from all *Siderastrea* samples (Figure 5). The ITS network indicated high diversity and two well-marked groups separated by at least 17 mutational steps for ITS, which correspond to *S. radians* and *S. siderea;* SRP54 network presented two groups separated by 16 mutational steps that have no correspondence with the groups observed for ITS; the CAG network presented fewer haplotypes and no evident structure (Figure 5). The ITS and SRP54 networks recover the BAPS groups, but blue and beige ITS groups did not present marked differences (Figure 5).

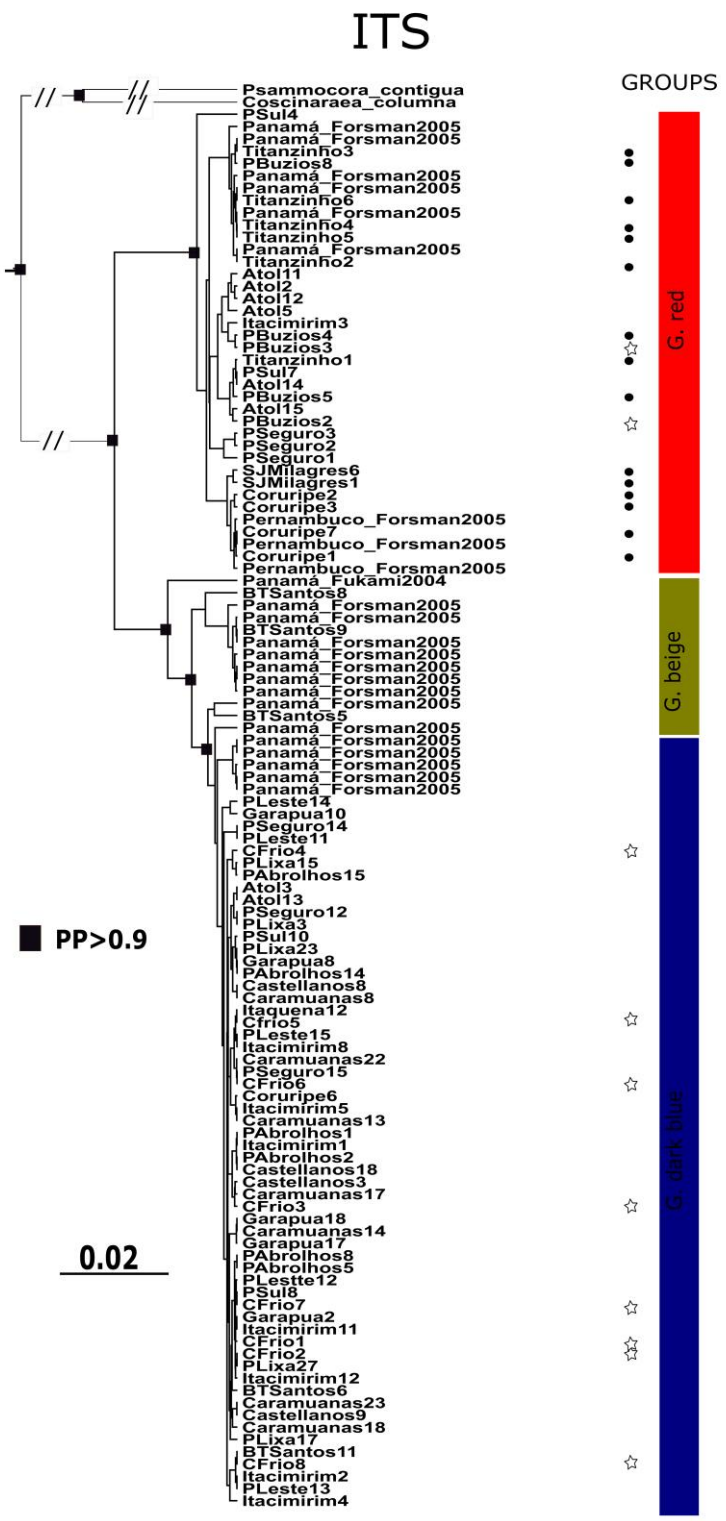

Figure 1. Bayesian phylogenetic inference for "*Siderastrea* Complex" using the molecular marker ITS; Posterior probabilities > 0.9 are indicated in black squares. Morphological identifications are represented by symbols ● = *Siderastrea radians*; ☆ = *S. stellata.*

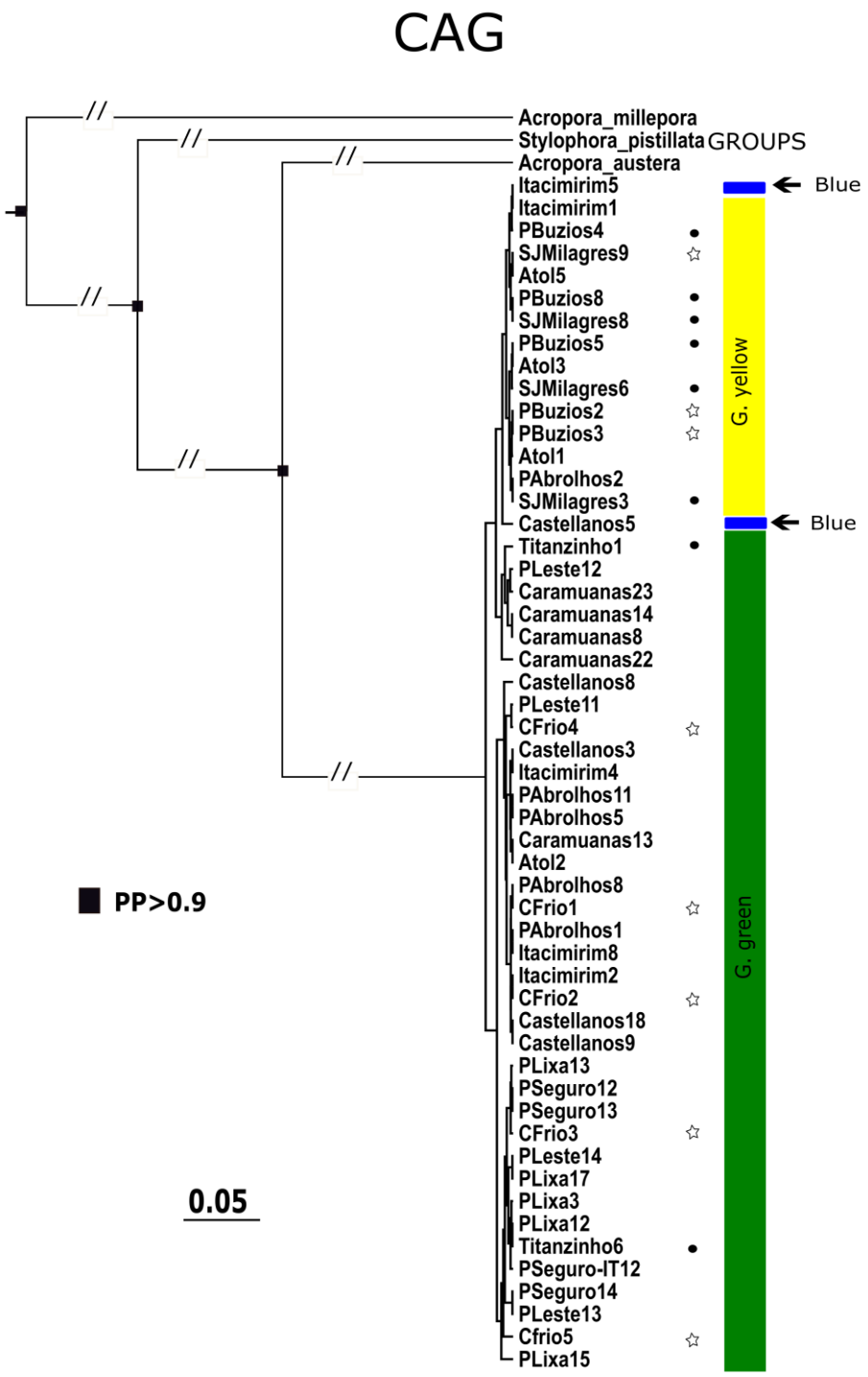

Figure 2. Bayesian phylogenetic inference for "*Siderastrea* Complex" using the molecular marker CAG; Posterior probabilities > 0.9 are indicated in black squares. Morphological identifications are represented by symbols ● = *Siderastrea radians*; ☆ = *S. stellata.*

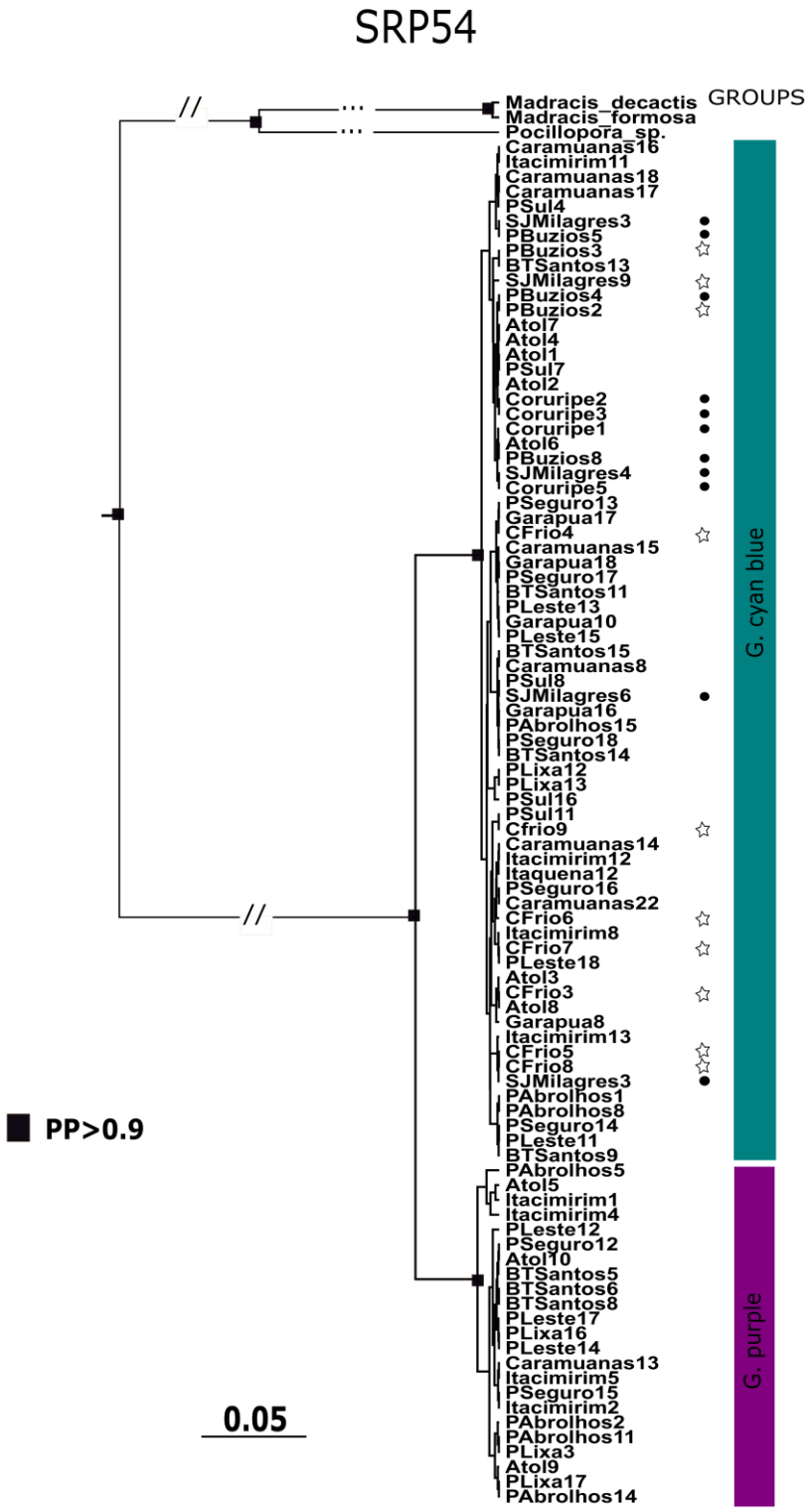

Figure 3. Bayesian phylogenetic inference for "*Siderastrea* Complex" using the molecular marker SRP54; Posterior probabilities > 0.9 are indicated in black squares. Morphological identifications are represented by symbols ● = *Siderastrea radians*; ☆ = *S. stellata.*

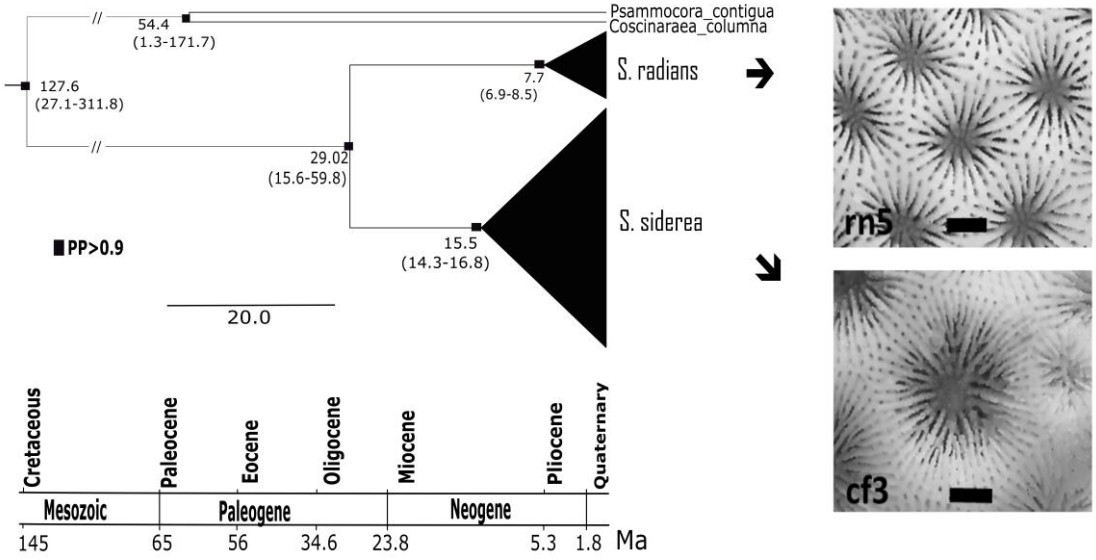

Figure 4. Multi-locus Time-calibrated Bayesian Inference of "*Siderastrea* Complex" using a concatenated dataset of the three molecular markers ITS, CAG and SRP54; The divergence times are shown in the main nodes, with 95% HPD in parentheses. Posterior probabilities > 0.9 are indicated in black squares.

Some geographical differentiation was observed among groups on the Brazilian coast (Figure 5). Although *S. radians* and *S. siderea* occur sympatrically (as detected in ITS analyses), the former is more frequent in the north, while the latter occurs mostly in the south (Figure 5). Curiously, the *S. siderea* beige group identified by BAPS occurs only in B. T. Santos and Panamá. The CAG groups also present this north-south disjunction and occurred sympatrically in some areas. SRP54 groups, however, have no clear geographical structure and both occur in most of the locations (Figure 5).

Pairwise Φ_{ST} values obtained for ITS, CAG and SRP54 sequences showed some differentiation among localities for *S. siderea* and *S. radians* (Table 3). However, no evidence of isolation by distance was detected (Figure 6).

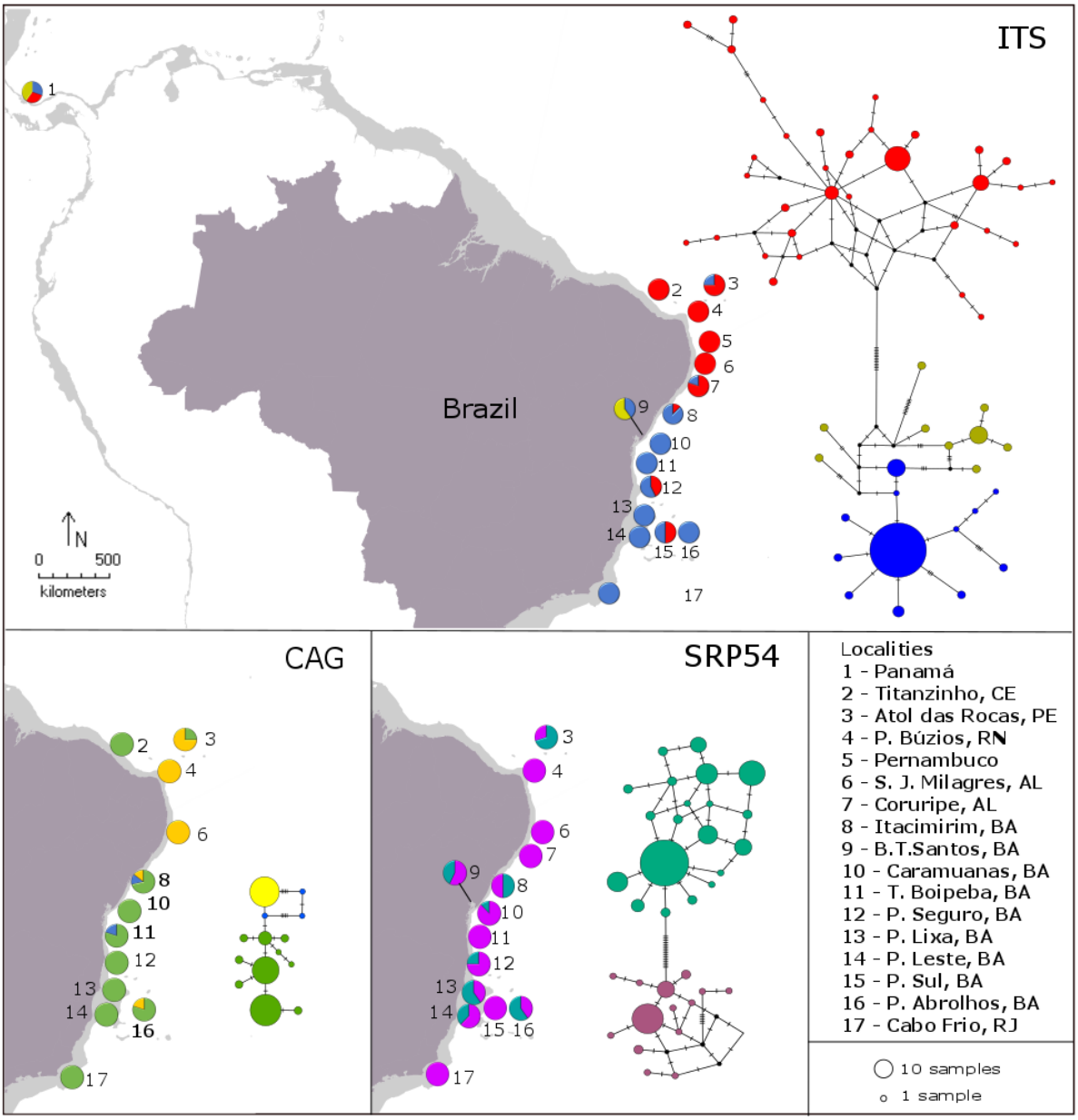

Figure 5. Median joining haplotype network for the three molecular markers, ITS, CAG, SRP54, using samples for the two species *Siderastrea radians* and *S. siderea;* circle sizes represent haplotype frequencies; colors on the haplotype networks represent genetic groups suggested by BAPS. The Pie Charts represent the frequency of genetic groups indicated by BAPS using samples for the two species, within sampling points; the numbers represent the sampling sites and the colors represent the groups inferred by BAPS for each marker. Colors: (ITS) red = *S. radians*, dark blue = *S. siderea*, beige = cluster in *S. siderea* (see Figure 1); (CAG) yellow = cluster I, green = cluster II, blue = cluster III; (SRP54) purple = cluster I, cyan blue = cluster II.

Table 2. Diversity indices and neutrality tests for *S. siderea* and *S. radians*. N = nº of individuals; S = nº of polymorphic sites; H = nº of haplotypes; Hd = haplotype diversity; π = nucleotide diversity; s.d. = standard deviation; *r* = Harpending's raggedness index; * = statistically significant values (p<0.05).

Localities	**N**	**S**	**H**	**Hd(s.d.)**	**π (s.d.)**	**D**	***FS***	**R**	**N**	**S**	**H**	**Hd(s.d.)**	**π (s.d.)**	**D**	***FS***	**r**
ITS – 573 bp	***S. siderea***								***S. radians***							
Panamá	15	27	8	0.82(0.05)	0.011(0.006)	0.12	3.3	-	6	2	3	0.55(0.14)	0.001(0.001)	-0.19	-0.3	-
Titanzinho, CE	-	-	-	-	-	-	-	-	6	1	2	0.3(0.145)	0.005(0.001)	-0.19	0.3	-
A. Rocas	2	0	1	0	0	0	0	-	6	8	8	0.94(0.05)	0.005(0.003)	0.12	-2.7*	-
P.Búzios, RN	-	-	-	-	-	-	-	-	5	8	8	0.96(0.06)	0.005(0.003)	0.12	-3.6*	-
Pernambuco	-	-	-	-	-	-	-	-	3	2	3	0.8(0.12)	0.002(0.002)	0.85	-0.08	-
S.J. Milagres, AL	-	-	-	-	-	-	-	-	2	4	3	0.83(0.22)	0.005(0.003)	1.4	0.46	-
Coruripe, AL	1	0	1	0	0	0	0	-	4	3	4	0.75(0.14)	0.002(0.002)	-0.2	-1.0	-
Itacimirim, BA	7	1	2	0.44(0.11)	0.001(0.001)	0	0.9	-	1	1	2	1(0.5)	0.002(0.003)	0	0	-
B.T.Santos, BA	5	16	4	0.8(0.09)	0.01(0.008)	1.2	4.4	-	-	-	-	-	-	-	-	-
Caramuanas, BA	7	6	4	0.58(0.14)	0.003(0.002)	-0.8	0.7	-	-	-	-	-	-	-	-	-
T. Boipeba, BA	9	6	3	0.63(0.06)	0.003(0.002)	-0.9	2.2	-	-	-	-	-	-	-	-	-
P. Seguro, BA	4	1	2	0.25(0.18)	0.0004(0.00)	-1.1	-0.9	-	3	6	3	0.8(0.12)	0.006(0.004)	1.3	1.9	-
P. Leste, BA	5	3	3	0.38(0.18)	0.002(0.001)	-0.5	0.3	-	-	-	-	-	-	-	-	-
P. Lixa, BA	5	2	3	0.62(0.14)	0.001(0.001)	0.02	-0.2	-	-	-	-	-	-	-	-	-
P. Sul, BA	2	2	2	0.67(0.2)	0.002(0.002)	1.89	1.5	-	2	6	3	0.83(0.22)	0.007(0.005)	1.7	1.1	-
P. Abrolhos, BA	6	1	2	0.48(0.1)	0.001(0.001)	0	1	-	-	-	-	-	-	-	-	-
C. Frio, RJ	8	2	3	0.57(0.11)	0.001(0.001)	0	0.3	-	-	-	-	-	-	-	-	-
Total	**76**	**46**	**24**	**0.78(0.02)**	**0.007(0.004)**	**-1.6***	**-4.27**	**0.03***	**38**	**40**	**36**	**0.93(0.02)**	**0.007(0.004)**	**-1.5***	**-23.8***	**0.01***
CAG – 227 bp	***S. siderea***								***S. radians***							
Panamá	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Titanzinho, CE	-	-	-	-	-	-	-	-	2	2	2	0.66(0.2)	0.01(0.01)	1.9	1.5	-
A. Rocas	1	0	1	0	0	0	0	-	4	4	2	0.53(0.2)	0.01(0.01)	1.8	3.2	-
P.Búzios, RN	-	-	-	-	-	-	-	-	5	0	1	0	0	0	0	-
Pernambuco	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S.J. Milagres, AL	-	-	-	-	-	-	-	-	2	0	1	0	0	0	0	
Coruripe, AL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Itacimirim, BA	5	8	3	0.6(0.13)	0.01(0.01)	0.16	3		-	-	-	-	-	-	-	-
B.T.Santos, BA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Caramuanas, BA	5	5	5	0.82(0.09)	0.01(0.01)	-0.33	-1.08		-	-	-	-	-	-	-	-
T. Boipeba, BA	4	0	1	0	0	0	0	-	-	-	-	-	-	-	-	-
P. Seguro, BA	4	0	1	0	0	0	0	-	-	-	-	-	-	-	-	-
P. Leste, BA	4	2	3	0.71(0.12)	0.004(0.003)	0.41	-.07	-	-	-	-	-	-	-	-	-
P. Lixa, BA	5	1	2	0.53(0.17)	0.002(0.003)	0.85	0.63	-	-	-	-	-	-	-	-	-
P. Sul, BA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. Abrolhos, BA	4	4	2	0.43(0.17)	0.01(0.01)	0.48	3.15	-	-	-	-	-	-	-	-	-
C. Frio, RJ	5	3	4	0.8(0.09)	0.01(0.004)	-0.6	-0.42	-	-	-	-	-	-	-	-	-
Total	**34**	**14**	**11**	**0.76(0.04)**	**0.01(0.01)**	**-1.2**	**2.8**	**0.2**	**12**	**4**	**2**	**0.54(0.12)**	**0.01(0.01)**	**1.7**	**3.7**	**0.7**
SRP – 54 233 bp	***S. siderea***								***S. radians***							
Panamá	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Titanzinho, CE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. Rocas	2	0	1	0	0	0	**0**		5	38	5	0.82(01)	0.08(0.05)	2.14	6.3	-
P.Búzios, RN	-	-	-	-	-	-	-	-	5	4	6	0.84(0.1)	0.007(0.005)	0.38	**-2.5***	-
Pernambuco	-	-	-	-	-	-	-	-	3	3	3	0.8(0.12)	0.007(0.006)	1.12	0.62	-
S.J. Milagres, AL	-	-	-	-	-	-	-	-	4	2	2	0.57(0.1)	0.005(0.004)	1.79	2.22	-
Coruripe, AL	-	-	-	-	-	-	-	-	2	3	3	0.83(0.22)	0.008(0.007)	1.09	0.006	-
Itacimirim, BA	7	38	5	0.83(0.06)	0.08(0.04)	1.97	9.35	-	-	-	-	-	-	-	-	-
B.T.Santos, BA	5	33	4	0.73(0.12)	0.07(0.04)	2.05	9.1	-	-	-	-	-	-	-	-	-
Caramuanas, BA	6	36	6	0.81(0.1)	0.05(0.03)	-0.43	3.42	-	-	-	-	-	-	-	-	-
T. Boipeba, BA	4	1	2	0.42(0.07)	0.002(0.002)	0.33	0.53	-	-	-	-	-	-	-	-	-
P. Seguro, BA	4	32	3	0.71(0.12)	0.08(0.04)	2.4	9.25	-	-	-	-	-	-	-	-	-
P. Leste, BA	5	34	5	0.82(0.1)	0.07(0.04)	1.96	5.77	-	-	-	-	-	-	-	-	-
P. Lixa, BA	2	1	2	0.5(0.27)	0.002(0.003)	-0.61	0.17	-	-	-	-	-	-	-	-	-
P. Sul, BA	1	0	1	0	0	0	0	-	-	-	-	-	-	-	-	-
P. Abrolhos, BA	6	42	7	0.88(0.8)	0.09(0.05)	1.5	4.16	-	-	-	-	-	-	-	-	-
C. Frio, RJ	7	4	4	0.58(0.14)	0.006(0.004)	0.02	0.1	-	-	-	-	-	-	-	-	-
Total	**49**	**52**	**22**	**0.79(0.03)**	**0.07(0.03)**	**0.8**	**4.8**	**0.05**	**19**	**38**	**12**	**0.87(0.3)**	**0.05(0.2)**	**0.61**	**3.4**	**0.2**

Table 3. Population pairwise Φ_{ST} for ITS, CAG and SRP54, respectively. *S. siderea* is below the diagonal and *S. radians* is above the diagonal. * = statistically significant values (p<0.05).

Localities	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
ITS – 573 bp																	
1-Panamá	0	0.82*	0.63*	0.55*	0.74*	0.58*	0.84*	0.89*	-	-	-	0.84*	-	-	0.71*	-	-
2-Titanzinho, CE	-	0	0.44*	0.54*	0.89*	0.55*	0.77*	0.89	-	-	-	0.80*	-	-	0.48*	-	-
3-A. Rocas	0.60*	-	0	0.32*	0.68*	0.46*	0.62*	0.46*	-	-	-	0.62*	-	-	0.34*	-	-
4-P. Búzios, RN	-	-	-	0	0.64*	0.40*	0.65*	0.52	-	-	-	0.64*	-	-	0.40*	-	-
5-Pernambuco	-	-	-	-	0	0.38*	0.67*	0.87*	-	-	-	0.81*	-	-	0.66*	-	-
6-S.J. Milagres, AL	-	-	-	-	-	0	0.39*	0.27	-	-	-	0.51*	-	-	0.26	-	-
7-Coruripe, AL	0.52*	-	1.00*	-	-	-	0	0.82	-	-	-	0.78*	-	-	0.51*	-	-
8-Itacimirim, BA	0.61*	-	0.80*	-	-	-	0.49	0	-	-	-	0.54	-	-	0.43	-	-
9-B.T.Santos, BA	0.37*	-	0.29*	-	-	-	0.03	0.43*	0	-	-	-	-	-	-		-
10-Caramuanas, BA	0.58*	-	0.51*	-	-	-	0.10	0.01	0.37	0	-	-	-	-	-	-	-
11-T. Boipeba, BA	0.61*	-	0.44	-	-	-	0.11	0.06	0.38	0.07	0	-	-	-	-	-	-
12-P. Seguro, BA	0.56*	-	0.92*	-	-	-	0.81*	0.14	0.39	0.06	0.18	0		-	0.59	-	-
13-P. Leste, BA	0.57*	-	0.74*	-	-	-	0.51*	0.16	0.41*	0.10	0.19*	-0.02	0	-	-	-	-
14-P. Lixa, BA	0.62*	-	0.65*	-	-	-	0.21	0.50*	0.32*	0.31*	0.16*	0.67*	0.57*	0	-	-	-
15-P. Sul, BA	0.58*	-	0.67*	-	-	-	0.11	0.60*	0.22	0.35*	0.26*	0.71*	0.58*	0.33*	0	-	-
16-P. Abrolhos, BA	0.59*	-	0.78*	-	-	-	0.41	-0.08	0.39	0.00	0.03	0.18*	0.17*	0.45*	0.56*	0	-
17-C. Frio, RJ	0.61*	-	0.68*	-	-	-	0.24	-0.03	0.42*	0.03	0.03	0.17	0.18*	0.37*	0.48*	-0.05	0
CAG – 227 bp																	
1-Panamá	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2-Titanzinho, CE	-	0	0.32*	0.87*	-	0.77*	-	-	-	-	-	-	-	-	-	-	-
3-A. Rocas	-	-	0	0.31	-	0.11	-	-	-	-	-	-	-	-	-	-	-
4-P.Búzios, RN	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-
5-Pernambuco	-	-	-	-	0		-	-	-	-	-	-	-	-	-	-	-
6-S.J. Milagres, AL	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-
7-Coruripe, AL	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-
8-Itacimirim, BA	-	-	0.21	-	-	-	-	0	-	-	-	-	-	-	-	-	-
9-B.T.Santos, BA	-	-	-	-	-	-	-		0	-	-	-	-	-	-	-	-
10-Caramuanas, BA	-	-	0.54*	-	-	-	-	0.19*	-	0	-	-	-	-	-	-	-
11-T. Boipeba, BA	-	-	1.00*	-	-	-	-	0.23	-	0.58*	0	-	-	-	-	-	-
12-P. Seguro, BA	-	-	1.00	-	-	-	-	0.25*	-	0.38*	1.00*	0	-	-	-	-	-

13-P. Leste, BA	**-**	-	0.87	-	-	-	-	0.26*	**-**	0.36*	0.83*	0.20	0	-	-	-	-
14-P. Lixa, BA	**-**	-	0.76*	-	-	-	-	0.12	**-**	0.16	0.57*	0.09	0.15	0	-	-	-
15-P. Sul, BA	**-**	-	**-**	-	-	-	-		-	-	-	-	-	**-**	0	-	-
16-P. Abrolhos, BA	-	-	0.54	-	-	-	-	0.06	-	0.28*	0.14	0.38*	0.36*	0.14	-	0	-
17-C. Frio, RJ	**-**	-	0.73*	-	-	-	-	0.16	-	0.37*	0.19*	0.29*	0.30*	0.12*	-	0.08	0
SRP – 54 233 bp																	
1-Panamá	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2-Titanzinho, CE	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3-A. Rocas	-	-	0	0.49*		0.42*	0.47*	-	-	-	-	-	-	-	0.37	-	-
4-P.Búzios, RN	-	-	-	0		0.05	0.28*	-	-	-	-	-	-	-	-0.08	-	-
5-Pernambuco	-	-	-	-	0	-	0.42*	-	-	-	-	-	-	-	0.11	-	-
6-S.J. Milagres, AL	-	-	-	-	-	0	-	-	-	-	-	-	-	-	0.04	-	-
7-Coruripe, AL	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-
8-Itacimirim, BA	-	-	0.34	-	-	-	-	0	-	-	-	-	-	-	-	-	-
9-B.T.Santos, BA	-	-	0.41*	-	-	-	-	-0.07	0	-	-	-	-	-	-	-	-
10-Caramuanas, BA	-	-	-0.05	-	-	-	-	0.21*	0.26*	0	-	-	-	-	-	-	-
11-T. Boipeba, BA	-	-	0.02	-	-	-	-	0.42*	0.50*	0.04	0	-	-	-	-	-	-
12-P. Seguro, BA	-	-	0.30	-	-	-	-	-0.08	-0.10	0.14*	0.41*	0	-	-	-	-	-
13-P. Leste, BA	-	-	0.99*	-	-	-	-	0.19	0.19	0.70*	0.99*	0.30	0	-	-	-	-
14-P. Lixa, BA	-	-	0.17	-	-	-	-	-0.02	-0.03	0.05	0.27	-0.10	0.40	0	-	-	-
15-P. Sul, BA	-	-	0.00	-	-	-	-	0.24	0.30	-0.23	-0.17	0.15	0.99	0.02	0	-	-
16-P. Abrolhos, BA	-	-	0.25	-	-	-	-	-0.05	-0.05	0.14*	0.34*	-0.09	0.25	-0.06	0.12	0	-
17-C. Frio, RJ	-	-	0.03	-	-	-	-	0.49*	0.58*	0.10	0.15*	0.50*	0.96*	0.37	-0.13	0.43*	0

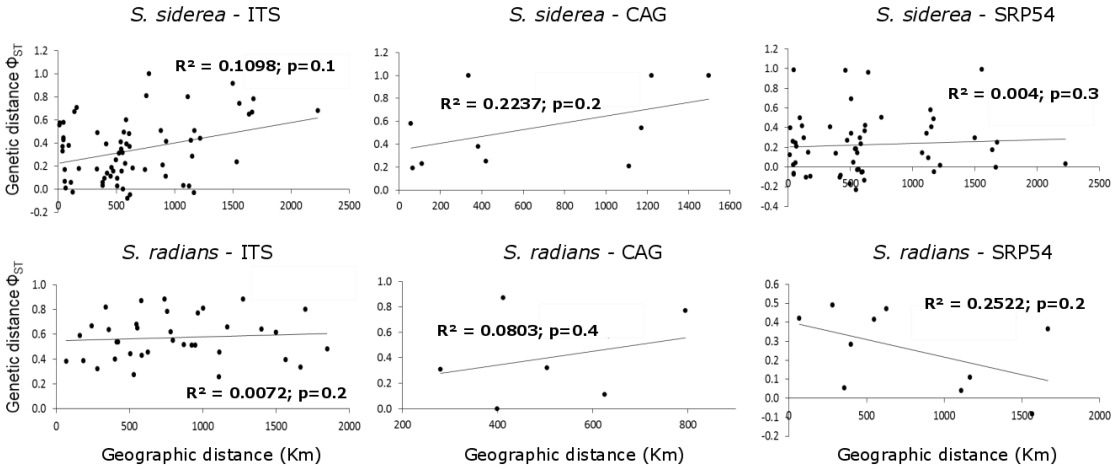

Figure 6. Mantel test for *Siderastrea radians* and *S. siderea* using the three molecular markers ITS, CAG and SRP54. The p-value and R² of each analysis are indicated in the graphs.

Demographic analysis

Tajima's D, Fu's *FS* and mismatch distribution analysis results for the ITS dataset indicated demographic expansion for *S. radians,* while only the first showed demographic expansion for *S. siderea*. The other markers showed no sign of expansion for any species (Table 2, Figure 7). The coalescent EBSP analyses presented a signal of demographic variation only for *S. radians* when ITS sequences were analyzed, indicating an expansion that started at ~2 Ma (Figure 8 and 9).

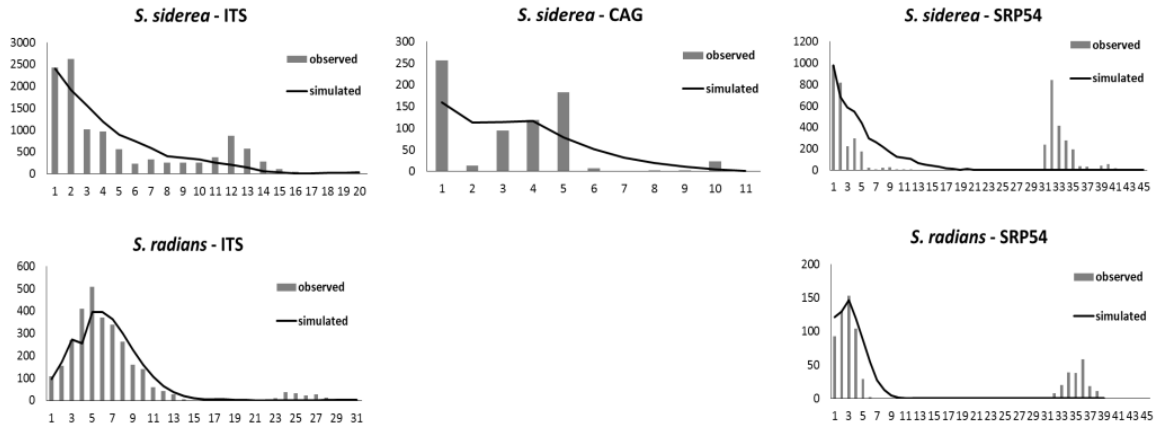

Figure 7. Mismatch distribution analysis for *Siderastrea radians* and *S. siderea* using the three molecular markers ITS, CAG and SRP54.

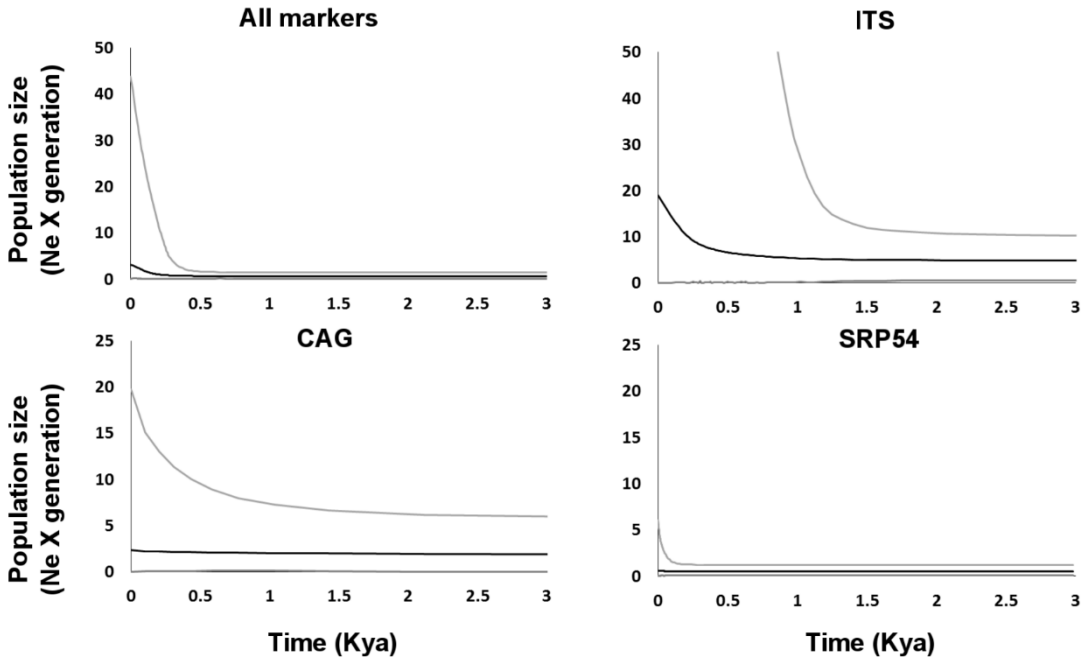

Figure 8. The demographic analysis Extended Bayesian Skyline Plot for *Siderastrea siderea* for all markers together and for each marker separately. Median shown in black line and the 95% HPD interval shown in gray line**.**

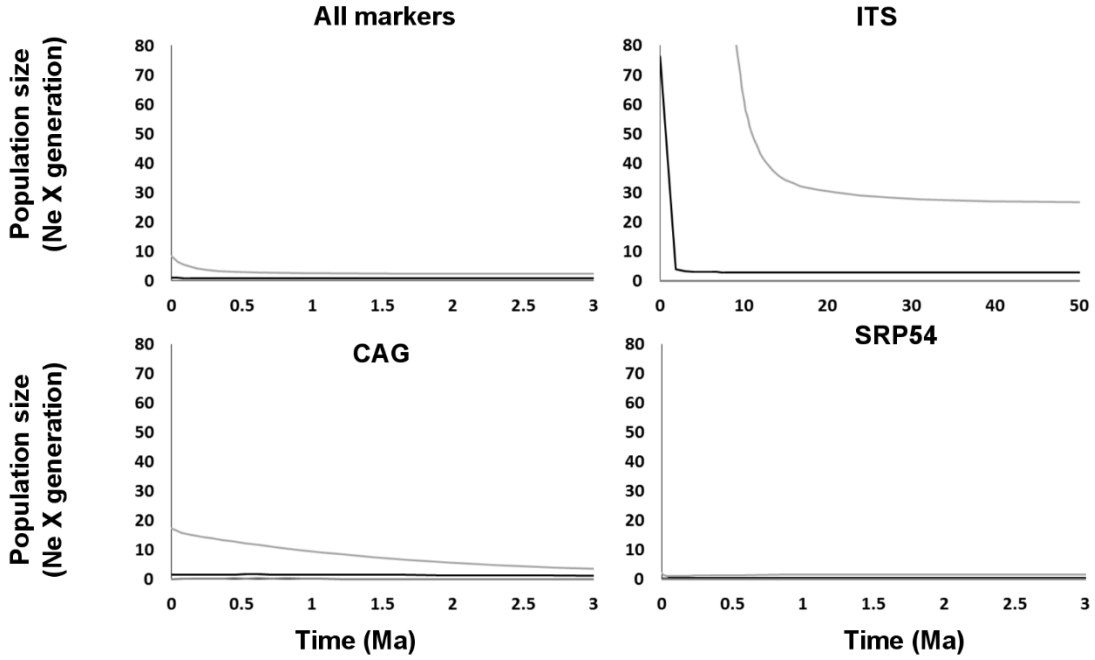

Figure 9. The demographic analysis Extended Bayesian Skyline Plot for *Siderastrea radians* for all markers together and for each marker separately. Median shown in black line and the 95% HPD interval shown in gray line**.**

Morphometry

In the morphometric analysis, we used a total of 65 samples from our study and one individual reported by Neves (2004) (Table 4). PCA showed high variation for the characteristics measured (Figure 10). The PC1 axis explained 47.11% of the variation and was primarily related to the characteristic Dcor, EspTec, DistCor, and Nsep (R = -0.50, -0.50, -0.45, -0.42, respectively). The PC2 axis explained 20% of the variation and was primarily linked to Dcol and Prof (R= - 0.76 and - 0.44, respectively). The scatterplot (Figure 10 – A (1)) showed high overlap among localities, although some of them display divergent morphologies. Colonies from B. T. Santos presented high values for Dcor, Nsep, EspTec, DistCor, but low values for Prof and Dcol. In turn, colonies from C. Frio also exhibited high values, but mainly for Prof and Dcol. The morphology of *S. siderea* (Neves 2004) was very different; however, it was closer to colonies from B. T. Santos. Pictures of the morphological variation evidenced in PCA can be observed in Figure 10 - B.

When the genetic groups of each marker were highlighted in PCA, (Figure 10 – A: 2, 3, 4), we observed that *S. siderea* ITS samples have higher values for each trait compared to *S. radians*, although some overlap was identified (Figure 10 – A: 2) . The CAG samples grouped in Cluster 1 exhibited predominantly low values, while Cluster 2 individuals have higher ones, also with some overlap (Figure 10 – A: 3) . For SRP54, we only have available samples from Cluster 1, which did not show a predominant pattern, instead appearing quite dispersed (Figure 10 – A: 4). Figure 10 – B illustrates corallites of 15 colonies measured and analyzed in PCA. This figure shows the high variability found in *Siderastrea*. Colonies cf4, cf3 and co6 are identified by ITS as *S. siderea*. Colonies rn8, rn5, co2, rn2, tit6, cor3 are identified by ITS as *S. radians*. The others, bts2, car2, ita9, bts8, sjm3 and ps6 did not have the genetic identification accessed.

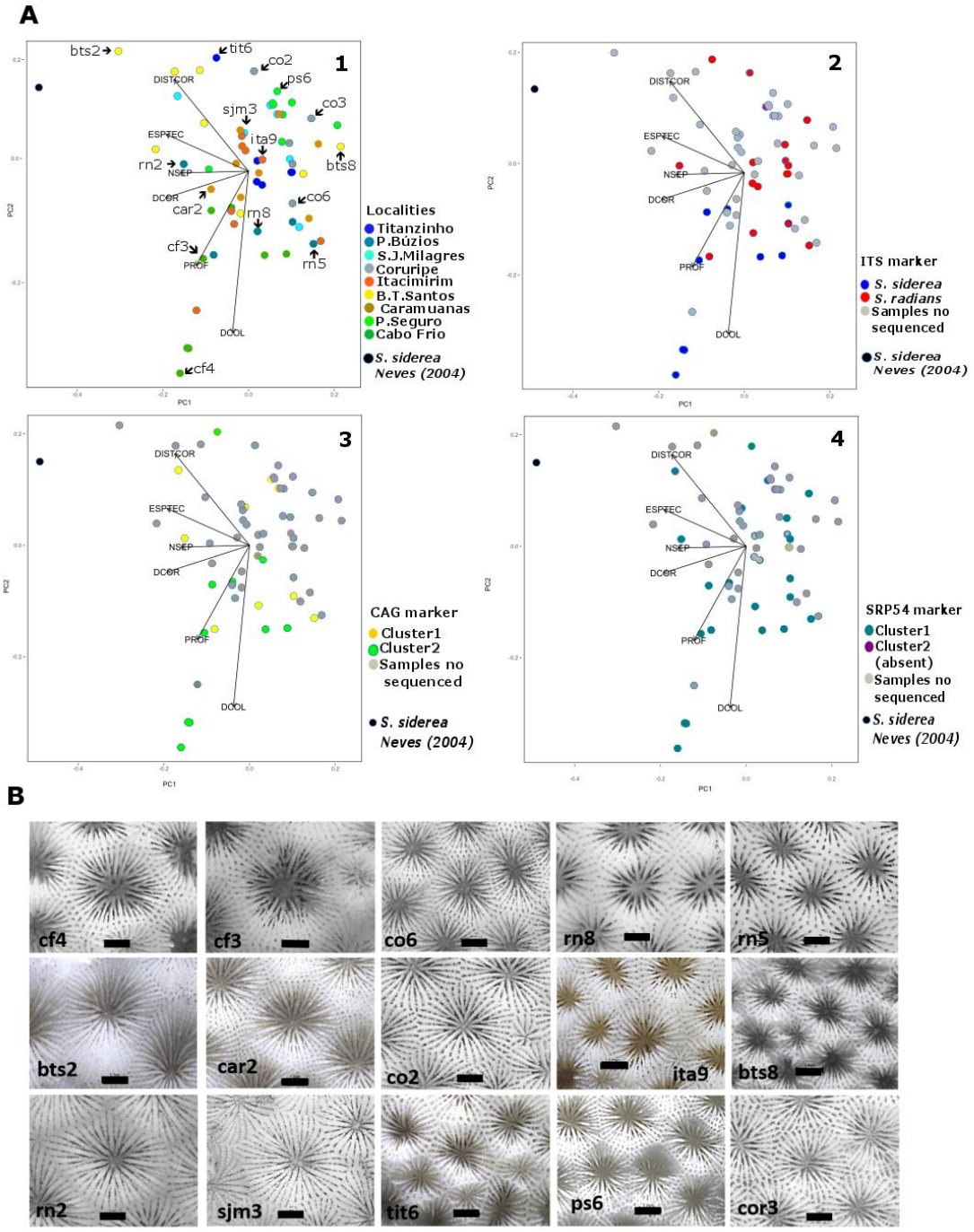

Figure 10. Morphological results. (A) Principal Components Analysis performed with six morphological traits of sampled colonies. Each point in the graph represents a colony. In (1), the graph is colored by localities, and acronyms represent corallites illustrated in B; in (2) the graph is colored by ITS groups; in (3) the graph is colored by CAG clusters of BAPS; in (4) the graph is colored by SRP54 clusters of BAPS. (B) Photography of corallites from different colonies with different morphology. They are indicated in A – 1. The acronym indicates the locality and the number of the individual: cf = Cabo Frio; co = Coruripe; rn = Rio Grande do Norte/P. Búzios; bts = Bahia de Todos os Santos; ita = Itacimirim; sjm = S.J. Milagres; ps = P. Seguro.

Table 4. Mean, standard deviation and amplitude of morphometric measures for localities that we have skeletal samples. corallite diameter (corD), columellar diameter (colD), septal number (sepN), thecal thickness (tecThick), columellar depth (depth), and the average distance between adjacent sampled calices (corDist). Metric values in millimeters.

Localities	Dcor	Dcol	Nsep	EspTec	Prof	DistCor
Titanzinho, CE	3.5 ± 0.38 (3 - 3.8)	0.4 ± 0.04 (0.3 - 0.4)	35.8 ± 2.5 (34 - 39)	0.4 ± 0.07 (0.4 - 0.6)	1.1 ± 0.06 (0.4 - 0.6)	0.9 ± 0.2 (0.8 - 0.9)
P. Búzios, RN	3.7 ± 0.77 (30 - 4.9)	0.5 ± 0.04 (0.4 - 0.5	34.2 ± 8.45 (26 - 42)	0.4 ± 0.09 (0.3 - 0.6)	1.2 ± 0.36 (0.7 - 1.6)	0.8 ± 0.14 (0.7 - 1)
S.J. Milagres, AL	3.3 ± 0.46 (2.9 - 4.1)	0.3 ± 0.1 (0.2 - 0.5)	36.1 ± 4.8 (29 - 41)	0.5 ± 0.06 (0.4 - 0.5)	1.2 ± 0.25 (1 - 1.7)	0.9 ± 0.12 (0.8 - 1.1)
Coruripe, AL	3.1 ± 0.19 (2.9 - 3.3)	0.3 ± 0.05 (0.3 - 0.4)	35.3 ± 1.13 (3.4 - 3.7)	0.4 ± 0.05 (0.4 - 0.5)	1.1 ± 0.15 (1 – 1.3)	0.8 ± 0.15 (0.7 - 1.1)
Itacimirim, BA	3.4 ± 0.35 (27 - 38)	0.5 ± 0.13 (0.4 - 08)	35.8 ± 4.46 (26 - 40)	0.5 ± 0.07 (0.4 - 0.6)	1.2 ± 0.16 (0.9 - 1.3)	1.0 ± 0.13 (0.8 - 1.2)
P. Seguro, BA	3.1 ± 0.31 (2.8 - 3.8)	0.3 ± 0.04 (0.3 - 0.4)	40.5 ± 5.21 (31 - 46)	0.4 ± 0.04 (0.3 - 0.5)	1.0 ± 0.13 (0.9 - 1.3)	0.9 ± 0.11 (0.7 - 1)
B.T. Santos, BA	3.8 ± 0.69 (2.7 - 4.6)	0.4 ± 0.05 (0.3 - 0.4)	46.1 ± 7.86 (33 - 51)	0.5 ± 0.11 (0.3 - 0.6)	1.2 ± 0.16 (1 - 1.4)	1.0 ± 0.3 (0.6 - 1.5)
Caramuanas, BA	3.3 ± 0.44 (2.7 - 4.2)	0.4 ± 0.04 0.3 - 0.4)	42.9 ± 4.73 (38 - 51)	0.4 ± 0.06 (0.3 - 0.5)	1.2 ± 0.1 (1.1 - 1.4)	0.8 ± 0.12 (0.6 - 1)
C. Frio, RJ	3.8 ± 0.27 (3.5 - 4.4)	0.5 ± 0.04 (0.4 - 0.6)	46.0 ± 3.37 (44 - 57)	0.4 ± 0.06 (0.3 - 0.6)	1.6 ± 0.58 (1 - 2.5)	0.8 ± 0.14 (0.6 - 1)
***S. siderea,* Panamá (Neves 2004)**	4	0.4	50	1	2	1.8

Discussion

This study provided information about the genetic and morphological diversity of *siderastreids* along the Brazilian coast, raising unexpected questions about the systematics of this complex group and suggesting a hypothesis about how the geographic history of the coast influenced the diversification of its current lineages. The results are based on an extensive data set including 16 sampling points along approximately 3000 km of the coast and additional information compiled from the literature. Despite some efforts, there are few molecular studies of Brazilian scleractinians with the approach and the amount of data we used here (Neves et al. 2008, Nunes et al. 2009, 2011, Peluso et al. 2018). Therefore, our study will contribute to the knowledge about the formation of Brazil's peculiar marginal reefs and highly endemic coral fauna.

Systematics considerations

The evidence of two genetic groups of *Siderastrea* along Brazilian coast evidenced by ITS sequences suport other studies of the literature (Neves et al. 2008, Nunes et al. 2011). However, the molecular comparison of our ITS sequences with the results of Forsman et al. (2005) indicates that the two genetic groups are very similar to the species *Siderastrea radians* and *S. siderea* described from the Caribbean and indicate no evidence of the third species, *S. stellata*, considered endemic of our coast.

These results support in part Neves et al. (2008), the first genetic study to define the occurrence of two genetic groups of *Siderastrea* for Brazil and not one, as previously thought. Our data agree with the occurrence and distribution of the two groups and with the record of *S. radians* for the Brazilian coast. However, our comparison with Caribbean samples identified the other group as *S. siderea,* while Neves and colaborators identified them as *S. stellata.* Neves et al. (2008) identified the species using morphological information; but they did not provide a genetic comparison with species from the Caribbean, leaving one gap in their work.

A very similar result to what we found for ITS was reported by Nunes et al. (2011) when they used the nuclear molecular markers β-tubulin and Pax-C to study dispersion and connectivity in Amphi - Atlantic corals, including *Siderastrea*. The authors pointed out that Brazilian siderastreids collected in three points along ~3000 Km of Brazilian coast were very similar to species from Panamá (in the Caribbean) and also denominate then as *S. radians* and *S. siderea*. They found evidence of hybridization and suggested that it could correspond to *S. stellata*; but they did not address this issue more deeply. Therefore, studies that used nuclear genetic markers up to the present day, including our and other works, have not indicated species differentiation of a third species of *Siderastrea* on the Brazilian coast.

On the other hand, our morphological results showed some differentiations between Brazilian and Caribbean species. While the Brazilian individuals genetically identified here as *S. radians* had considerable correspondence with taxonomical morphs, the samples genetically identified as *S. siderea* had a discrepant morphology when compared with the original diagnosis and with specimens from the

Caribbean (Neves 2004) (Figure 1 and 8). Individuals collected here present small and irregular corallites and intratentacular budding, known as corresponding to the description of *S. stellata,* as can be seen in Figure 8 and Table 3 (Neves et al. 2010). Thus, we also detected different morphotypes in Brazil, as proposed by other authors (Vaughan 1919, Neves et al. 2010), despite the genetic similarity with the Caribbean species.

Incongruences among morphological and genetic data in scleractinian species are very common in the literature. They are usually explained by high phenotypic plasticity, incomplete lineage sorting, hybridizations and combinations of these factors (Forsman et al. 2009, Budd et al. 2010). In the case of Atlantic *Siderastrea*, factors suggested as reasons for speciation between groups from the Caribbean and Brazil, such as environmental differences, the Amazon River geographical barrier and/or just spatial distance could be important for morphological differentiation, or to induce genetic structure between the regions as observed by Nunes et al. (2011). Nevertheless, they were probably not sufficient to promote a complete speciation on the Brazilian coast. Indeed, new records of *Siderastrea* in mesophotic communities of the Amazon river mouth (Cordeiro et al. 2015) suggest that this barrier to dispersion could be less effective than was expected, mainly for this group.

Recently, a molecular and morphologic study of *Siderastrea* using samples restricted to Veracruz Reef System National Park reported individuals similar to *S. stellata* (Gulf of México; García et al. 2017). The molecular analysis of this study was based on two ITS nuclear regions. When they used the same ITS region used in our work, they defined all samples as *S. radians*. When they used the ITS2 region, they observed three well-defined genetic groups with congruence with the morphology of the three species *S. siderea*, *S. radians* and *S. stellata.* Given the high phenotypic plasticity and dispersal ability observed for Atlantic *Siderastrea* (Neves et al. 2008, Neves et al. 2010, Nunes et al. 2011), the occurrence of *S. stellata*–like morphotypes in Mexico is reasonable.

CAG and SRP54 sequences could not be compared to Caribbean samples because we do not have data from this region; however, these markers added intriguing data to our study. The lack of monophyly among groups and little

congruence with both the ITS dataset and morphological identification (Figure 1, 2, 3 and 10) suggest two possibilities. First, the incongruence among markers could indicate incomplete lineage sorting, a common pattern that was also suggested for other species of corals (Willis et al. 2006). Second, it might indicate the existence of hybridization and/or introgression among species. Hybridization and introgression were confirmed for many broadcast-spawning corals such as *S. siderea* (van Oppen et al. 2000, Vollmer and Palumbi 2002, Arrigoni et al. 2016, Hellberg et al. 2016). However, this process has few records in brooding corals such as *S. radians,* and it was only reported for *Madracis, Pocillopora* and *Styllopora* (Miller and Ayre 2004, Flot et al. 2008, Frade et al. 2010).

Our molecular dating indicated a divergence between *S. radians* and *S. siderea* in the late Oligocene (Figure 1), which makes the incomplete lineage sorting hypothesis less probable, although this alternative cannot be ruled out. In turn, *S. radians* and *S. siderea* are sibling species with sympatric and syntopic occurrence (Figure 5); thus, hybridization between the species is plausible, although no ecological experiments have demonstrated it so far. Both hybridization and incomplete lineage sorting are in agreement with the high morphological variation observed in Brazilian siderastreids and could explain the morphological overlaps between *S. radians* and *S. siderea* (Figure 10), commonly discussed in the literature (Yonge 1935, Foster 1980, Zlatarski and Estalella 1982, Menezes et al. 2013, 2014).

All of this information highlights the importance of a wide taxonomic revision of Atlantic siderastreids. Our data also indicate the need to take into account the proximity between *S. siderea* and *S. stellata*. Forsman et al. (2005) proposed a close relationship between *S. radians* and *S. stellata* based on one sample from Pernambuco, on the northeastern coast of Brazil, were *S. radians* is predominant. However, at that time, they did not know about the occurrence of two species in Brazil, and they treated *S. stellata* as the only and endemic species of our coast. The inclusion of broad sampling throughout the Atlantic Ocean will also help to better understand the taxonomy and geographical distribution of these lineages. *Siderastrea* has a wide distribution in the Atlantic Ocean and most molecular studies include too few points. In the Central Atlantic, for example, studies are usually centered on Panamá. Finally, the use of cutting-edge molecular methods, including

next-generation sequencing and advanced analysis techniques, associated with micro and macro morphological structures, could also help to clarify these taxonomic difficulties.

Phylogeographic patterns

Time-calibrated analysis indicated that the divergence between the two genetic groups found on the Brazilian coast, *S. radians* and *S. siderea,* occurred at ~29.02 Ma (95% HPD = 15.6-59.8 Ma) (Figure 4). Several studies suggest that, during this period, the earth was undergoing important environmental transitions due to tectonic and climatic events (Potter and Szatmari 2009, Smart and Murray 1994). In the Atlantic Ocean, studies indicate that an increase in regional planktonic productivity would have increased due to continental shelves' progradation (Smart and Murray 1994, Edinger and Risk 1995), changes in ocean temperature and circulation (Nisancioglu 2003) and sea level fluctuations (Rossetti et al. 2013). According to Budd (2000), who analyzed Caribbean fossil coral reefs, the Late Oligocene to Earliest Miocene (28 ± 24 Ma) is one of the five known periods of extinction followed by diversification in Caribbean coral reefs. This information supports the idea that the genetic groups found in our study may have emerged during this period. However, it is difficult to indicate which of the various environmental and geological events caused this differentiation based only in our data.

The predominance of *S. radians* in the north and *S. siderea* in the south along Brazilian coast, with sympatric and syntopic occurrence in some places, was also observed in other studies with siderastreids (Neves et al. 2008). Other marine groups also indicate the presence of this barrier (Souza et al. 2017, Picciani et al. 2017), although it is not a rule (Peluso et al. 2018). This pattern has been attributed to the drainage of the São Francisco River, which causes a salinity and sediment barrier on the coast, and to the anticlockwise oceanic gyre that reaches the Brazilian shore between 8ºS and 10ºS and bifurcates, forming the Brazilian Current to the south and the Northern Brazilian Current to the north (Carvalho and Kikuchi 2013). Other evidences are necessary to associate these events with *Siderastrea* diversification, but these events apparently limited the distribution of *S. radians* and *S. siderea* and indicate a niche differentiation between them. It is possible that *S.*

radians individuals hardly crossed the São Francisco barrier and that they develop better in higher temperatures of low latitudes, while *S. siderea* could tolerate the lower temperatures that occur from the resurgence of the Central Waters of the South Atlantic at approximately 22º S, near Arraial do Cabo (Stramma and England 1999, Neves 2004).

Regarding intraspecific variation, the results showed absence of diversity gradients or areas with higher variability. Consequently, we detected no signs of recent colonization from the Caribbean, as observed for other marine organisms (Rocha 2003, Souza et al. 2017); or from possible Pleistocene coral reef refugia in submerged seamounts near Abrolhos Bank, as hypothesized by (Leão 1983) and evidenced by recent results with other groups (Pinheiro et al. 2017, Peluso et al. 2018). However, these data agree with the possibility that the species may have maintained their latitudinal amplitude of occurrence during the last sea level fluctuations.

Stratigraphic studies on different coasts around the world (eg. Gulf of Mexico and Gulf of Papua) reveal the presence of terraces of coralgal reefs at around 60 and 90 m deep along the slopes of the continental shelf (Droxler and Jorry 2013, Khanna et al. 2017). According to these studies, the terraces were constructed near the coast during “windows of opportunity” promoted by punctuated rises in sea levels since the last glacial maximum. Kikuchi and Leão (1998) described reef structures at about 80 m deep in Brazil; however, this issue has rarely been explored since. It could be that the known resistance of siderastreids’ to environmental variation (Lirman et al. 2002, Castillo et al. 2014, Horvath et al. 2016) may have favored the occupation/building of these terraces over time while less resistant corals may have been restricted to refugia in regions far from the coast, as indicated for *Mussismilia hispida* by Peluso et al. (2018). However, further studies are necessary to investigate the presence of Brazilian terraces and their possible influence on scleractinian populations during geological time.

Alternative explanations for the absence of diversity gradients in our data are related to the reproductive traits and ecological population structure of Brazilian siderastreids. Previous studies suggest that, despite the brooding behavior of both Brazilian species, which favors structure by phylopatric settlement (i.e., offspring

grow near to progenitor colonies), moderate gene flow has been observed for both species (Neves et al. 2008, Nunes et al. 2011). Neves and Silveira (2003) also described that larvae of *S. stellata* could remain approximately 15 days in the water column, facilitating migration between distant populations. These factors could promote genetic homogeneity along the coast and decrease differences among localities. Additionally, the probable presence of colonies with different ages in our samples due to indeterminate growing of corals could mask a possible spatial genetic structure. The attempt to standardize colony sizes as an age estimate is imprecise since coral can usually fuse, fractionate or undergo partial mortality (Sebens 1982). However, this cohort overlap is inherent in most coral populations and present in most studies (Veron 1995).

The occasional occurrence of a different group of *S. siderea* in B. T. Santos and Panamá (Figure 5) is intriguing. An introduction event of a different *S. siderea* genetic group could perhaps explain this isolation. B. T. Santos has ~1200 km^2 of calm waters and is known for the presence of important vectors of invasion, such as three commercial ports, oil platforms, anchorage points and intense ship traffic ever since the great navigations in the 16th century (Amado-Filho et al. 2008). The literature describes some exotic species in this bay (Gerhardinger et al. 2006, Almeida et al. 2015), with recent reports of invasive corals (*Tubastraea tagusensis* and *Tubastraea coccinea* - (Sampaio et al. 2012). Considering the high resistance of *Siderastrea* and the presence of incrusting forms, the introduction of a different genetic group of *S. siderea* cannot be ruled out.

The demographic analyses for all markers together have not indicated recent expansion since the Last Glacial Maximum, and this agrees with the hypothesis that siderastreids may have followed the displacement of the sea level over this time, keeping their latitudinal range. However, the demographic analysis using only ITS shows that *S. radians* indicated demographic expansion since early Pleistocene, while the demography of *S. siderea* has remained constant. The probable distinct ecological niches between species may have influenced these contrasting results. While *S. radians* is more restricted to shallow and warm water (Laborel 1969, Neves 2004), *S. siderea* has eurybathic and eurythermic distribution (Laborel 1969/70, Lirman et al. 2002, Castillo et al. 2014, Horvath et al. 2016,

Cordeiro et al. 2015). Shallow regions, where *S. radians* is frequent, are much more vulnerable to geologic events such as sea level changes (Karhng et al. 2010, Lindfield et al. 2016, Bongaerts et al. 2017), which may be reflected in the higher population fluctuation over time.

Conclusion

Our study indicated that Brazilian siderastreids are very similar to their Caribbean congeners *S. siderea* and *S. radians*, suggesting that *S. stellata* could represent a morphological variation of *S. siderea*. The genetic diversity, structure and demography of both species showed no evidence of recent colonization from the Caribbean or dispersion from a possible Pleistocene refuge in submerged seamounts near Abrolhos Bank, which suggests that *Siderastrea* species may have maintained their latitudinal amplitude of occurrence during sea level fluctuation over geological time. Indeed, new stratigraphic evidence of deep coralgal terraces on the slopes of continental shelf's seems to support this hypothesis. We highlight the need for a taxonomical revision of this group using wide genetic and morphological sampling throughout the Atlantic Ocean and further investment in more polymorphic markers to confirm the biogeographic pattern found. This study contributes to the knowledge about the historical process responsible for the distribution of current Brazilian marginal coral reef biodiversity.

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CAPÍTULO II

Paleoclimatic distribution and phylogeography of *Mussismilia braziliensis* (Anthozoa; Scleractinia), and endemic coral of Brazilian reefs

Abstract

Several studies suggest that Pleistocene glacial cycles and sea level variations drastically affected shallow and near shore ecosystems such as coral reefs. For the Southwest Atlantic, a submarine mountain chain near Abrolhos Bank has been proposed as a region of climatically stable refugia during the Last glacial Maximum (LGM), from where our present Brazilian reefs received propagules. Here, we integrated Paleoclimatic simulations based on ecological niche models (ENM) and a phylogeographic approach to access this hypothesis for the endemic and important reef building coral *Mussismilia braziliensis*. The niche modeling indicated a reduction in the potential distribution of this species from present to LGM; however, contrary to what was expected, the predicted climatically stable regions were not located in the Victoria – Trindade mountain chain, but in regions to the north of this chain, where the species currently occurs. Genetic data showed low structure for the three markers used, SRP-54, ITS and MaSC-1, and no sign of recent demographic expansion. Our results suggested a scenario where *M. braziliensis* probably followed the sea level variation, maintaining the amplitude of its latitudinal distribution since LGM, and was not confined to a reduced climatic refugium as previously imagined. We highlight the pioneering nature of this study in trying to comprehend the historical processes related to the formation of the current scleractinian biodiversity in Brazilian reefs.

Introduction

Several works suggest that glacial cycles occurred throughout the Pleistocene (2.5 Ma – 11 thousand years before present) and caused important changes in the marine ecosystems (Ludt and Rocha 2014). There are signs that these events may have altered ocean currents, changed water column thermal dynamics and modified sea level (which dropped as much as 120 m during the Last Glacial Maximum - LGM) affecting shallow and near-shore ecosystems such as coral reefs (Molengraaff and Weber 1937, Benzie 1999, Veron 1995, Pellissier et al. 2014, Ludt and Rocha 2014, Renema et al. 2016). Few pleistocenic extinctions have been reported for marine organisms, in comparison with other past geological periods (Ludt and Rocha 2014); however, some authors indicate that this period had one of the highest extinction rates of scleractinian corals in the Mid-Atlantic Ocean (Budd 2000, Johnson et al. 1995).

Some coral reef habitats have been pointed out as refugia based on their climate stability during the Pleistocene (Ludt et al. 2012, Pellissier et al. 2014). Refugia may be defined as habitats that provide shelter from environmental stressors or advantages in biotic interactions, permitting a local long-term persistence of populations (Tzedakis et al. 2013, Keppel et al. 2012, Gavin et al., 2014, Kavousi and Keppel 2017). Refugia have an important role in avoiding species extinction, acting as bases for the recolonization of more unstable areas and allowing enough time to generate areas with a high diversity (McKenna and Farrell 2006; Carnaval et al. 2009; Pellissier et al. 2014b). Evidence of refugia in the Indo – Pacific ocean have been of great importance in explaining the current pattern of reef diversity (Ludt et al., 2012, Bowen et al., 2013, Cowman et al. 2017).

For the South Atlantic ocean, where reef formations extend mainly in a north-south direction along ~3000 Km of Brazilian coast (Leão et al. 2003), the influence of Pleistocene climatic oscillations on coral diversity is still poorly explored (Leão 1983, Peluso et al. 2018). This region is known for its narrow continental shelf (an average width of 50 km) and turbid waters because of riverine water drainage, coastal erosion and sediment re-suspension (Leão and Dominguez 2000, Castro and Pires 2001, Leão et al. 2003, Segal et al. 2008). Zooxantellate corals have low species richness, with 21 species described; however, these regions have a remarkable endemism rate

(Neves et al. 2006). Additionally, the predominance of ancient massive morphs, in spite of the more recent porous and branched morphology known in Caribbean Acroporids (Pandolfi and Jackson 2006), is an interesting feature of Brazilian species.

Some authors proposed that the presence of archaic morphs preserved on the Brazilian coast occurs because of the existence of a refugium near Abrolhos Bank during the low sea level in the Pleistocene (Leão 1983, Nunes et al. 2008). This region is known for its enlargement of the continental shelf (~200 km width) and for the presence of the Vitória - Trindade submarine mountain chain away from and perpendicular to the shoreline (Leão et al. 2003, Pinheiro et al. 2014). According to those authors, these distant habitats allowed corals to remain protected from coastal environmental variation (mainly sedimentation) during the Pleistocene glacial periods. The increase in the sea level caused a displacement of preserved fauna in refugia to the current continental shelf, and the archaic traits of a tertiary coral fauna were conserved (Leão 1983). Despite the scientific importance of this hypothesis, there are few subsequent studies exploring it for corals (Peluso et al. 2018).

The genus *Mussismilia* is known for massive colonial forms, corallites that are discrete or arranged in short series, discontinuous columela with trabecular linkage and abundant vesicular endotheca (Budd et al. 2012). It was considered a member of the Mussidae Family, but has recently been transferred to the Favinnae Subfamily, and it is now a sister of groups previously considered Faviidae (Nunes et al. 2008, Budd et al. 2012, Schwartz et al. 2012). The genus is composed of four living species, *Mussilimila hispida* (Verrill, 1901), *M. harttii* (Verrill, 1868), *M. braziliensis* (Verrill, 1868), *M. leptophylla* (Verrill, 1868) and two extinct species registered in the Mediterranean basin, *M. provincialis* Matheron 1900 and *M. vindobonensis* Chevalier 1961. Fossils of the living *Mussismilia* were found along several Mid – Atlantic deposits during periods known for great environmental changes, such as the Miocene, Pliocene and early Pleistocene (Budd et al. 1999, Budd 2000, Klaus et al. 2011, 2012). Currently, the genus is locally extinct in this region, but represents a paleoendemic group of Brazilian reefs (Cowman et al. 2017). Indeed, some experimental studies indicate that it can adapt well to sediment-dwelling environments found on the Brazilian coast (Loiola et al. 2013). The endemic

condition of *Mussismilia* on the Brazilian coast is an intriguing question and could be related to the presence of Pleistocene refugia; however, few studies have directly addressed this issue before (Peluso et al. 2018).

Currently, different approaches of ecological niche modeling (ENM) and paleoclimatic simulations, based on coupled atmosphere-ocean models (AOGCMs), such as PMIP3 (Paleoclimate Modeling Interface Project), have been used to assess the species ranges across space and time and to build a hypothesis about the influence of past climate change on species diversity. These approaches have been largely applied to terrestrial *taxa* explorations to identify Pleistocene climate change influences on vertebrates and invertebrates (Carnaval et al. 2009b; Peres et al. 2015), detect retraction or expansion of biomes and their old connections (Carnaval and Moritz 2008, Leite et al. 2016, Sobral-Souza et al. 2015). However, these approaches have been under-used in studies of the influence of paleoclimate changes on sea *taxa*, such as corals.

In addition, phylogeographic methods have used spatial patterns of genetic polymorphism sampled from present-day populations to infer the evolutionary history of population dynamics (Avise 2009). Coupled with ENM and paleoclimatic simulations, this approach can provide a powerful tool to study the diversification processes that give rise to current populations (Beheregaray 2008, Gavin et al. 2014). In Brazil, some phylogeographic studies showed interesting patterns for fishes, crustaceans, cnidarians and polychaetes (Stampar et al. 2012, da Silva et al. 2016, Neves et al. 2016, Souza et al. 2016, Nunes et al. 2016, Hurtado et al. 2016, Peluso et al. 2018).

In this work, we integrated ENM and phylogeographical approaches to investigate the existence of coral reef refugia around Abrolhos Bank during the Pleistocene, using *Mussismilia braziliensis*. This species is called “the Brazilian brain coral” and is one of the main builder corals at the top of the “chapeirões” (mushroom-shaped outcrops) of Brazilian reefs (Leão et al. 2003). However, it is confined to a very restricted zone of ~800 km around Abrolhos Bank, and some evidence shows that it is currently subject to anthropic and climatic threats (Leão et al. 2008, Francini-Filho et al. 2008, Garcia et al. 2013, Leão et al. 2016, Mazzei et al. 2016). Our specific objectives were (1) build ENM predictions to compare the past (LGM – 21ka)

and the current *Mussismilia braziliensis* potential distribution, (2) access genetic diversity and population structure throughout the species' geographical distribution, (3) infer phylogenetic relationships and divergence time among populations (4) and estimate their demographic history. We hypothesized the existence of Pleistocene spatial refugia in the submarine mountain chain near Abrolhos Bank, with more genetic diversity and ancient lineages in reefs from this region, and signs of demographic reduction in the Pleistocene followed by recent population expansion. We emphasize that this is the first study that combines Paleoclimatic Modeling and Phylogeographic approaches to explore the evolutionary history of Brazilian scleractinian corals.

Material and methods

Present and Paleodistribution models

We used ENM approaches to build the current distribution and the paleodistribution of *Mussismilia braziliensis*. Usually, ENM techniques infer correlations between environmental variables (climate) and current known occurrence points to predict the environmental conditions tolerated by a species, to plot suitability values in other locations where the species is not-known (Franklin and Miller 2010, Peterson *et al.* 2011). Three major pillars for building ENM are listed: (i) species occurrence (ii) climate variables and (iii) mathematical algorithms (Peterson et al. 2011).

We obtained occurrence records of *Mussismilia braziliensis* in the OBIS dataset (Ocean Biogeographic Information System - available in http://www.iobis.org). Also, we included records of our samples in field observation of *M. braziliensis* and current records of its recent expansion in distribution (Mazzei et al. 2016), totalizing 1058 known occurrence points (Supplementary information 1).

The climate and paleoclimate variable layers, used to infer the species distribution, were downloaded at MARSPEC database (Ocean Climate Layers for Marine Spatial Ecology available at https://www.marspec.org) (Sbrocco and Barber 2013). This database has 18 sea environmental data items (derived from salinity, temperature and physical characteristics) for current and past (LGM) scenarios. However, these variables are auto-correlated and a variable assortment was

necessary. We chose layers with 5 arc minutes, ~10 km resolution (in the Equator region), and we clipped them to the Western Atlantic Ocean with an extent of (75º and 30ºW longitude and 35ºS and 15ºN latitude). We used this background as the studied area, considering the historical and current species dispersion capability, two criteria described by Barve et al. (2011) for background selection. We applied a factorial analysis, with *Varimax*, to choose variables that vary more throughout the study area (similar to the strategy adopted by Sobral-Souza et al. 2015). The chosen variables were Plan curvature (Biogeo3), Profile curvature (Biogeo4), Mean annual SSS (psu) (Biogeo8), Annual range in SSS (psu) (Biogeo11), SST of the warmest month (°C) (Biogeo15), Annual range in SST (°C) (Biogeo 16). We included bathymetry, although it has not been selected in this analysis, because of its biological importance for coral reef distribution (Veron 1995)

The occurrence points and selected climatic variables were used to build ENM generated under the current climate scenario and predicted for the 21 Ka (LGM) climate scenario. We used five mathematical algorithms that are based on different methods and premises in order to increase the reliability of models based on a forecast ensemble approach (Araujo and New 2007). Three of them are based only on presence records: (1) envelope score, Bioclim (Nix 1986); (2) Mahalanobis distance (Farber and Kadmon 2003) and (3) Domain—Gower distance (Carpenter et al. 1993); and two are machine-learning methods based on presence/background records: (4) Support Vector Machines (SVM) (Tax and Duin 2004); and (5) Maximum Entropy (MaxEnt) (Phillips and Dudík 2008).

We used a bootstrap method to randomize the occurrence points into 75-25% train-test subsets to evaluate the models. As these subsets are correlated, we performed the bootstrap procedure 20 times to decrease data co-linearity. We calculated the ‘maximum sensitivity and specificity threshold’ for each model to compute the continuous map in binary maps. We used this threshold because is the best when using presence-only methods in the ENM approach (Liu et al. 2011, 2013). Based on this threshold value, we also estimated the True Skill Statistic (TSS), an accuracy measure to evaluate presence–absence distribution models (Allouche et al. 2006). We considered TSS values higher than 0.5 (Allouche et al. 2006). Finally, we computed a consensual map with the frequency of each grid cell

predicted from all accurate models (a similar method to that used in (Sobral-Souza et al. 2015).

Sample collection

We sampled fragments of *Mussismilia braziliensis* (~5 cm) from five sites throughout its distribution (Table 1). We used a hammer and chisel to remove them, taking care to minimize damage to the whole colony. We scraped the fresh tissue from the living surface, put it in vials of 1.5 ml containing anhydrous alcohol or guanidine thiocyanate solution (4 M guanidine thiocyanate, 0.1% N-lauroyl sarcosin sodium, 10 mM Tris pH8, 0.1 M 2-mercaptoethanol) and stored it at freezing temperature until extraction. All individuals sampled were under permits granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, permit nos. 39090).

DNA extraction, amplification and sequencing

Genomic DNA was extracted using a phenol protocol described by (Nunes et al. 2009). Three nuclear markers were used. The Signal Recognition Particle 54-kDa region (SRP54) was amplified using primers SRP54Madfor and SRP54Madrev2 (Frade et al. 2010), and the thermal profile had initial denaturation step at 94°C for 2 min; 35 cycles at 94°C 2min, 52°C for 30 s and 72°C for 1 min; and extension at 72°C for 2 min. The Internal Transcribed Subunit region (ITS) was amplified using primers ITS-1 and ITS-4 (White et al. 1990), and the thermal profile had an initial denaturation step at 96°C for 2 min; 35 cycles at 95°C for 10 s, 52°C for 30 s and 70°C for 4 min; and extension at 70°C for 2 min. The *MaSC-1* was amplified using primers 3-550 F and 3-550 R (Macdonald et al. 2011), and the thermal profile had initial denaturation step at 95°C for 4 min; 35 cycles at 95°C for 45 s, 62°C for 45 s and 72°C for 2 min; and extension at 72°C for 10 min. All PCR reactions were carried out with a total volume of 25µl with 10 ng of genomic DNA, 3.0 mM $MgCl_2$, 1X of taq buffer, 0.4 mM of dNTP, 0.16 µM of each primer, 1U of Taq DNA polymerase and milli-q water.

The amplicons were analyzed in a Perkin-Elmer Prism 377 capillary sequencer. Sequences were aligned using the MUSCLE algorithm (Edgar 2004), and manually edited in MEGA 6.0 (Tamura et al. 2013). Heterozygous sites were coded

agreeing with IUPAC ambiguity codes. Phased haplotypes were previously estimated using a Bayesian method employed in PHASE (Stephens and Donnelly 2003), based on the input files prepared with Dnasp v. 5.0 (Librado and Rozas 2006). The gametic phases were inferred with a minimum posterior probability of 0.9, usually recommended to reduce the number of unresolved haplotypes with false positives (Garrick et al. 2010).

Haplotype networks, genetic diversity and population structure

We constructed haplotype networks in PopART v. 1.77 (Leigh and Bryant 2015), using a Median-joining algorithm (Bandelt et al. 1999). Molecular diversity indices, haplotype frequencies and pairwise differentiations among sample sites (Φ_{ST}) were calculated using Arlequin v. 3.5 (Excoffier & Lischer, 2010). Isolation-by-distance was calculated using GeneAlEx v. 6.5 (Peakall and Smouse 2012). An analysis of molecular variance, AMOVA, with three levels, was conducted to compare percentage of variance among localities and among regions (North: Itacimirin and Caramuanas; and South: P. Seguro, P. Leste, P. Abrolhos) using Arlequin v. 3.5. (Excoffier et al. 1992). We also applied a Bayesian Analysis of Population Structure - BAPS v. 6.0 (Corander et al. 2008) to estimate the most probable number of genetic groups in our data (k) in a range between 1 and 20.

Phylogenetic inference and divergence time

We constructed independent Bayesian inference trees for each marker using BEAST v.1.7.4 (Drummond et al. 2012a). The best fit nucleotide substitution models selected by Akaike Information Criterion (AIC) in MEGA 6.0 was JC for ITS4 and *MaSC-1* (Tamura et al. 2013). Sequences of *Favia fragum* (JX452177.1, JX452166.1, GQ 152790.1) and *Favia pallida* (JF785617.1) available in the GenBank database were used as outgroup to root the trees because of the phylogenetic proximity with *Mussismilia* (Schwartz et al. 2012). A time-calibrated phylogenetic tree was inferred for both markers separately, using a previous mutation rate found in the literature (0.004 for ITS – Savard et al. 1993; $6.77E^{-4}$ for *MaSC-1* - Schwartz et al. 2012). We also used information from fossil records of the genus *Mussismilia* and of the outgroups *F. pallida* and *F. fragum* that first appeared in the paleontological basin around 23.03, 20.43 and 5.33 Ma bp respectively (Chevalier 1961, Perrin et al.

1998). We inferred parameters from a run of 200 million steps sampled every 10,000 steps. Convergence and effective sample sizes (ESS>200) were checked in Tracer (Rambaut and Drummond 2009), and the first 2000 trees were discarded as burned. The program Figtree 1.4.2 was used to draw the resulting MCC tree (Rambaut 2009).

Demographic analysis

Historical demographic processes were inferred using neutrality tests Tajima's D (Tajima 1989), Fu's Fs (Fu 1997) and mismatch distribution analysis (Harpeding 1994) for markers and each location in Arlequin v. 3.5. We also estimated posterior distributions of population size (Ne) through the time for both markers separately using the Extended Bayesian Skyline Plot analysis (EBSP) implemented in Beast v. 1.7. (Drummond and Rambaut 2007). We used the same substitution model and mutation rate as for phylogenetic analysis. Runs of 200 million interactions were conducted with samples being taken every 10,000 generations.

Results

All the obtained models presented high values of TSS and consequently, high accuracy (Supplementary information 3). We observed a clear difference between *Mussismilia braziliensis* distribution from present and Last Glacial Maximum (LGM) (Figure 1). The models from current climate scenario (0 k – Figure 1) pointed that *M. braziliensis* is potentially restricted to the Eastern region of the Brazilian coast (10° to 20°S). In turn, the paleoclimatic models for LGM indicated a great reduction in the potential distribution of the species (21 k before today – Figure 1). According to this paleoclimatic model, during LGM, the continental shelf where reefs occur today was exposed to the atmosphere and *M. braziliensis* were potentially restricted to small areas near this region.

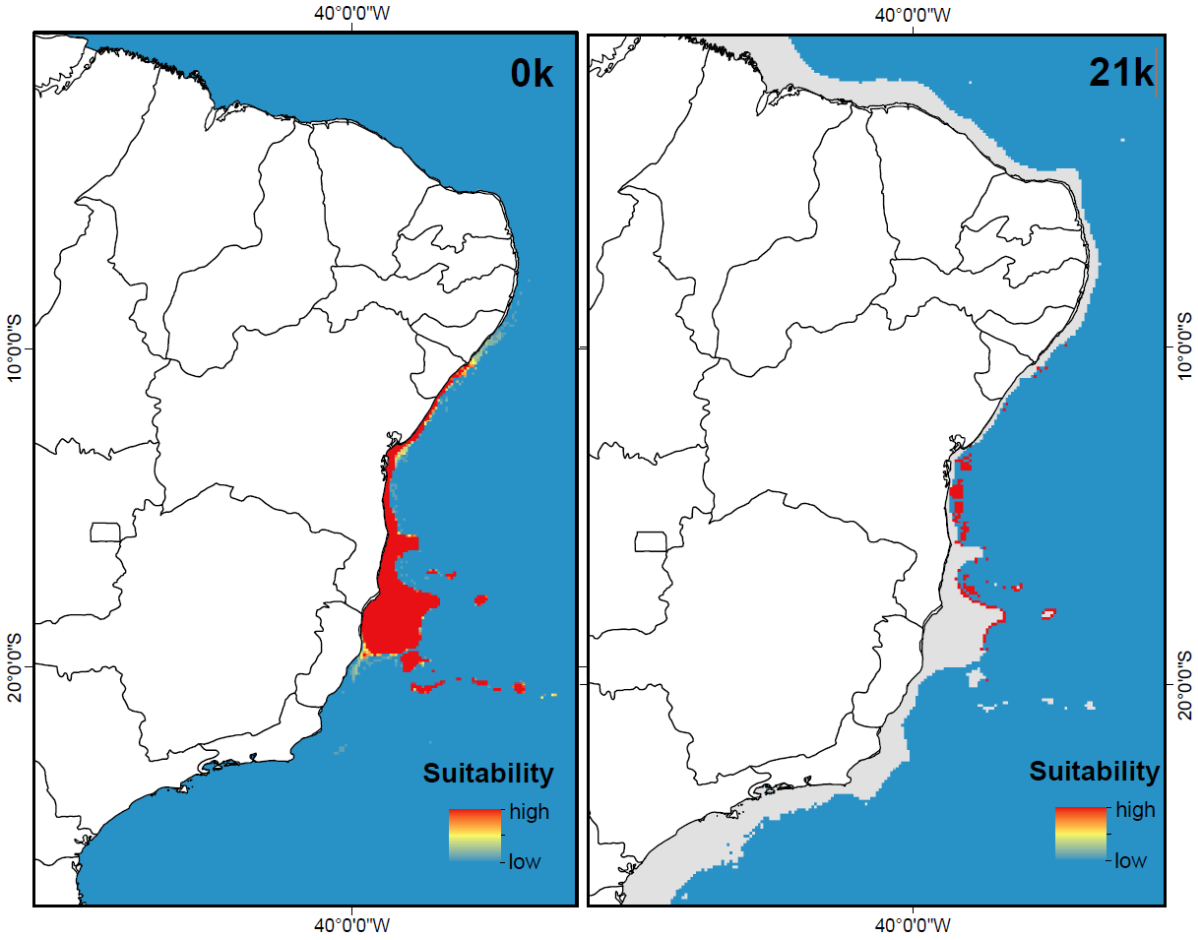

Figure 1. Modeled distributions of *Mussismilia braziliensis* for present (0k) and LGM (21k) scenarios. In the left figure (0k), the continental shelf is submerged. In the right figure (21k), the continental shelf is exposed and represented by a gray band along the coast. Suitability means how suitable the environment is for the occurrence; the values are based on an ensemble of the five used algorithms Bioclim, Mahalanobis, Domain-Gower, SVM and MaxEnt.

Genetic diversity, haplotype networks and population structure

Sequences of ITS presented 619 bp, and *MaSC-1* presented 274 bp with 6 and 5 polymorphic sites, respectively, and no gaps (Table 1). Both markers showed ambiguous peaks and, because of this, we applied haplotype reconstruction conducted in PHASE. The analysis resulted in 8 solved sequences for ITS and 9 for *MaSC-1* with posterior probability higher than 0.9. Sequences of SRP54 presented 358 bp; however, they were monomorphic.

The haplotype and nucleotide diversity is described in Table 1. The ITS marker showed higher molecular diversity when compared to *MaSC-1*; however, no

geographic structure was observed in both markers. The ITS network indicated a wide dispersion of haplotypes among localities with few exclusive haplotypes in each locality (Figure 2). Regarding the *MaSC-1* network, it presented low variation with two common haplotypes widely distributed along sampled places and presented few mutational steps between groups indicated by BAPS (Figure 2).

Pairwise F_{ST} values were not significant among localities when we analyzed ITS, but showed some significant differentiation between P. Abrolhos and other places when *MaSC-1* was observed (Table 2). Isolation-by-distance (IBD) was not detected for both markers (Figure 4). The AMOVA showed that the highest percentage of genetic variation for both markers is within populations, with ~82% for ITS and ~94% for *MaSC-1* (Table 3).

Phylogenetic inference and divergence time

Phylogenetic Bayesian inference for ITS and *MaSC-1* did not recover the same topology, and they presented low posterior probability nodes along the terminals (Figure 5). The groups indicated by BAPS for *MaSC-1* were not recovered in phylogeny. Time calibrated analysis using ITS and *MaSC-1* presented different mean values, but they occurred in the same confidence interval (Figure 5). Divergence time from the outgroup occurs in 31.52 Ma (95% highest posterior density 'HPD' = 18.48-79.92 Ma – Figure 5) for ITS and 23.17 Ma (95% HPD = 19.51–41.01 Ma – Figure 5) for *MaSC-1,* while the species diversification occurred in 4.62 Ma (95% HPD 0.54-18.04Ma – Figure 5) and 9.13 Ma (95% HPD 2.8 – 17.7 Ma – Figure 5) for ITS and *MaSC-1,* respectively.

Demographic analysis

Fu's FS detected demographic expansion in ITS for the most distant localities, Itacimirim and P. Abrolhos and for total data (Table 1). However, the other analysis did not detect any historical demographic fluctuations (Table 1 - Figure 7).

Table 1. Diversity indices and neutrality tests for *Mussismilia braziliensis*. N = nº of individuals; S = nº of polymorphic sites; H = nº of haplotypes; Hd = haplotype diversity; π = nucleotide diversity; s.d. = standard deviation; * = statistically significant values (p<0.05).

	ITS							***MaSC-1***						
Location	N	S	H	Hd (s.d.)	π (s.d.)	D	FS	N	S	H	Hd (s.d.)	π (s.d.)	D	FS
Itacimirim	4	4	6	0.89 (0.11)	0.003 (0.002)	0.9	-2.8*	6	5	3	0.53 (0.14)	0.006 (0.005)	0.32	2.03
Caramuanas	5	3	5	0.87 (0.07)	0.002 (0.001)	1.0	-1.5	5	5	3	0.51 (0.16)	0.005 (0.004)	-0.33	1.48
P. Seguro	2	3	4	1(0.18)	0.003 (0.002)	0.2	-2.2	4	4	5	0.86 (0.11)	0.008 (0.005)	1.59	-1.04
P. Leste	-	-	-	-	-	-	-	2	4	3	0.83 (0.22)	0.008 (0.007)	-0.07	0.25
P. Abrolhos	7	5	9	0.95 (0.04)	0.003 (0.002)	1.5	-4.4*	7	0	1	0	0	0	0
Total	18	6	13	0.9 (0.02)	0.003 (0.002)	0.8	-6.3*	24	5	6	0.49 (0.08)	0.006 (0.004)	0.94	0.27

Table 2. Population pairwise Φ_{ST} for *Mussismilia braziliensis*. ITS is below and *MaSC-1* is above the diagonal.

	Itacimirim	Caramuanas	P. Seguro	P. Leste	P. Abrolhos
Itacimirim		-0.09373	0.03633	0.21197	0.18933*
Caramuanas	-0.03		0.0833	0.28469	0.14563
P. Seguro	0.16	0.13		-0.10121	0.54424*
P. Leste	-	-	-		0.82170*
P. Abrolhos	0.02	0.05	0.02	-	

Table 3. Hierarchical analysis of molecular variance (AMOVA) was used to estimate levels of genetic differentiation among populations (F_{ST}), between groups of populations or regions (F_{CT}) and between populations within regions (F_{SC}).

Source of variation	ITS d.f.	Sum of squares	Variance components	Percentage of variation	MaSC-1 d.f.	Sum of squares	Variance components	Percentage of variation
Groups	2	3.222	0.09683 Va	9.86	2	2.783	-0.13786 Va	-17.47
Population within groups	1	0.567	-0.04031 Vb	-4.11	2	6.084	0.27954 Vb	35.42
Within population	32	29.600	0.92500 Vc	94.24	43	21.708	0.64748 Vc	82.05
Total	35	33.389	0.98151		47	36.708	0.78916	
Fixation indexes:	F_{SC}: -0.04557; F_{ST}: 0.05758; F_{CT}: 0.09865				F_{SC}: 0.30155; F_{ST}: 0.17953; F_{CT}: -0.17469			

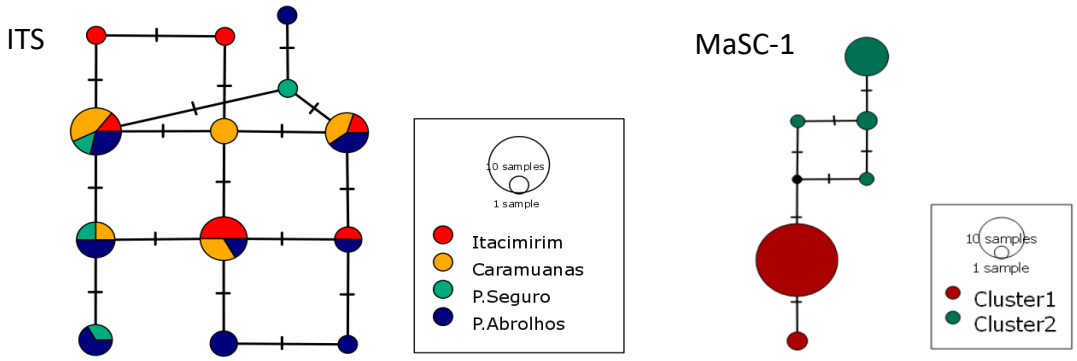

Figure 2. Median joining haplotype network for both markers. Colors represent sampling localities for ITS and groups inferred by BAPS for MasSC-1. Circle sizes represent haplotype frequencies.

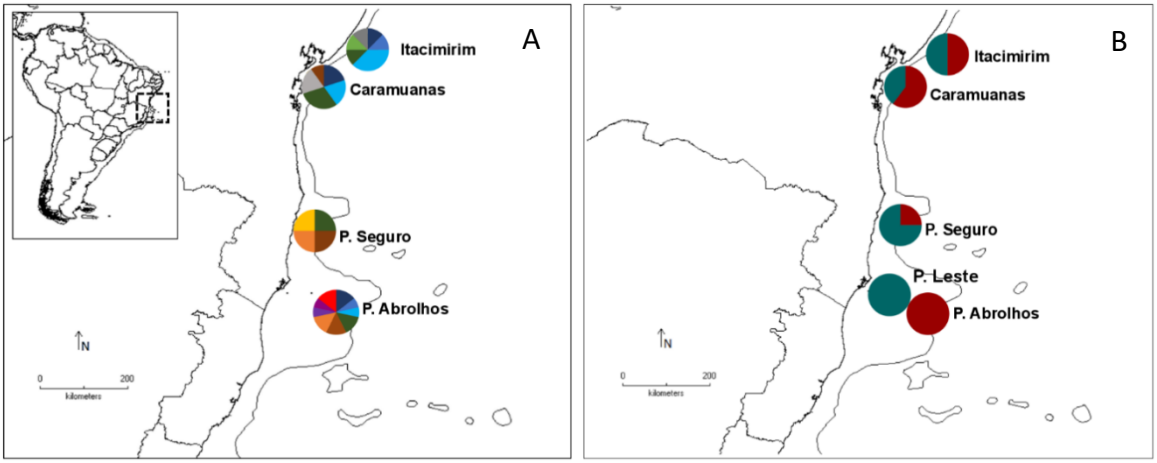

Figure 3. Pie chart indicating the diversity distribution along sampling points. (A) Frequency of haplotypes of ITS (B) Frequency of genetic groups indicated by BAPS for MaSC-1.

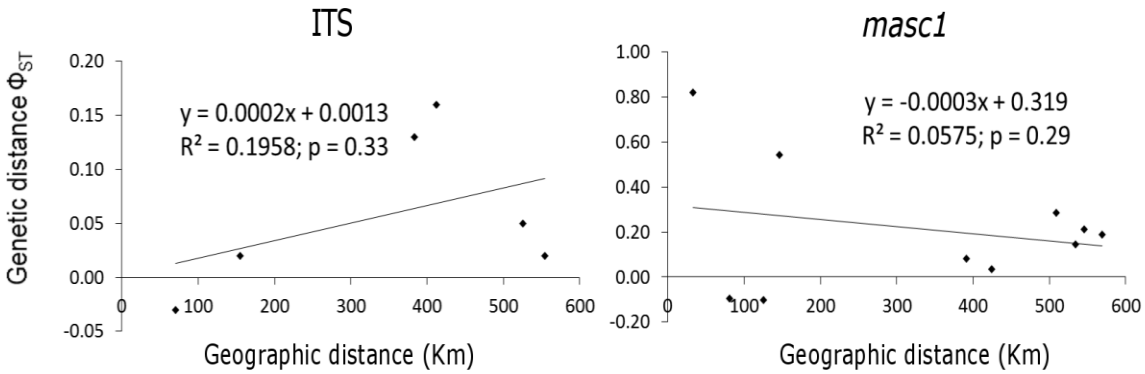

Figure 4. Mantel test for *Mussismilia braziliensis* using ITS and MaSC-1. The R^2 and p-value of each analysis are indicated on the graph.

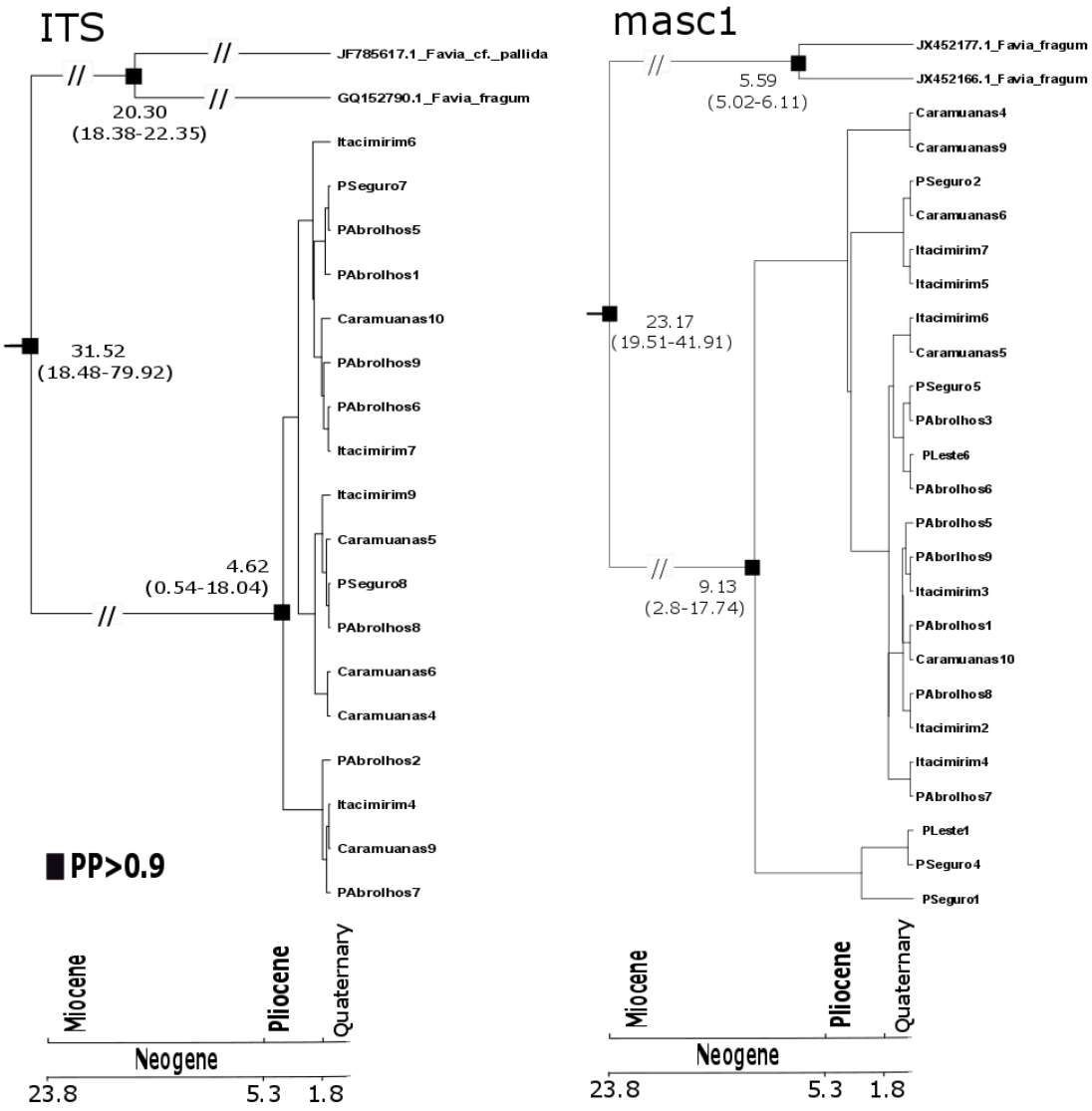

Figure 5. Bayesian phylogenetic inference for ITS and MaSC-1 sequences. The divergence times of the main nodes are shown, with 95% HPD in parentheses. Posterior probabilities > 0.9 are indicated in black squares.

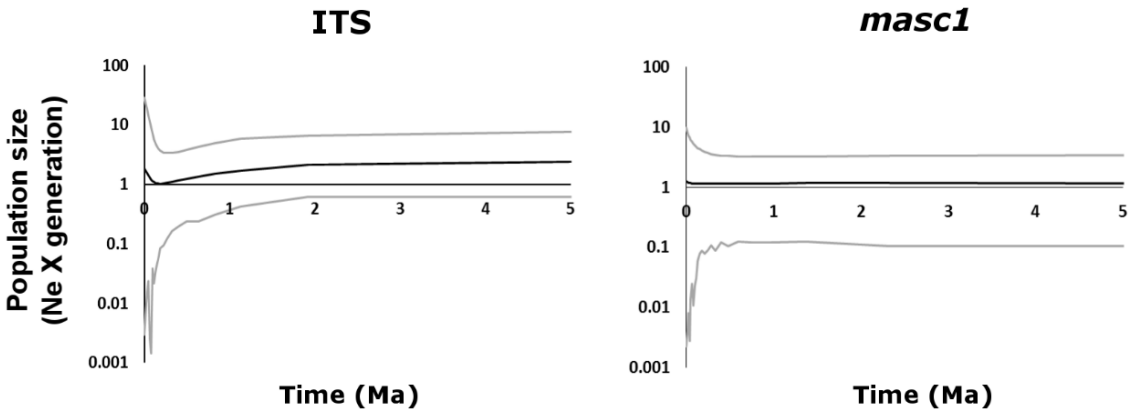

Figure 6. The demographic analysis Extended Bayesian Skyline Plot for *Mussismilia braziliensis* for ITS and MaSC1, with the median shown in the black line and the 95% HPD interval shown in the gray line.

Discussion

Paleoclimatic modeling

Our ENM models indicate a reduction of *Mussismilia braziliensis* potential distribution from the present (0k) to LGM (21k) and suggest that this species was restricted to a small area along the coast during glaciation times. The models are in accordance with the hypothesis of refugia near the Abrolhos region (Leão 1983); however, contrary to what was expected by this author, at least in LGM, the predicted stable regions were not located in the Victoria-Trindade mountain chain, but in northern regions near to the coast and seamounts of Minerva, Rodgers and Hotspur.

This results are unexpected since regions near to the coast are usually more subject to sedimentation than more distant regions, and we expected that seamounts away from the coast would have been more favorable to reef growth (Dutra et al. 2006, Leão e Kikuchi 2005). This hypothesis has been supported in the case of some species (Pinheiro et al. 2017, Peluso et al. 2018). However, some geological studies have described the occurrence of deep biogenic structures on the slopes of the continental shelf that probably were formed during punctuated sea level rises since the LGM (Droxler and Jorry 2013, Khanna et al. 2017). Some species may have been able to occur at these sites. In Brazil, (Kikuchi and Leão 1998) reported evidences of biogenic structures in oceanic slopes at a depth of around 80 m; other biogenic

structures were also reported in deep sectors to the north of Abrolhos Bank (Bastos et al. 2013, Bastos et al. 2016). Further studies with a detailed description of these areas can help to understand the formation of the current diversity in this region.

Another interesting pattern is that the latitudinal amplitude of occurrence of the species presented very little, but interesting, variation. From LGM to the present, *M. braziliensis* apparently expanded its potential distribution slightly to the south. According to the environmental layers used in this study (Supplementary information 2), the annual temperature variation around Abrolhos Bank 18°40'59.49"S/38°59'33.94"W decreased from LGM to the present. High variations in the temperature can prejudice the metabolism of many species (Sheppard et al. 2009), and this could perhaps explain the low suitability of *M. braziliensis* in the south of Abrolhos bank in LGM. The other environmental characteristics around the coast of Bahia are apparently very peculiar, and this condition did not shift much along the latitudinal gradient during the time period studied.

Genetic diversity and population structure

Each marker studied presented very different diversity. The absence of variation found for Srp54 is in agreement with a possible demographic reduction of this species, whereas this marker has shown itself to be quite variable for other coral species (Frade et al. 2010, Concepcion et al. 2008). On the other hand, ITS and *MaSC-1* presented the common diversity observed for these markers in corals (Saavedra-Sotelo et al. 2011, Goodbody-Gringley et al. 2012, Schwartz et al. 2012).

The low population structure, the indication that a major part of variation is within localities (Table 1 and 3) and the absence of isolation-by-distance do not corroborate the hypothesis of colonization from Pleistocene refugia in submerged seamounts near Abrolhos Bank (Leão 1983). However, it can be suggested that the hypothesized refugia did not change the latitudinal amplitude of geographical occurrence over geological time. These data are also in agreement with our ENM results, which indicated a reduction in the area of potential distribution, but not in latitudinal amplitude. As discussed before, the possibility of occurrence of coral species along the coast and not restricted to small refugia from LGM cannot be

rejected, and studies to identify these structures should be carried out, in order to better understand the formation of current coral diversity.

The low genetic structuring observed can also be justified by traits related to the life history of *Mussismilia braziliensis*. This species has annual and synchronic reproductive cycles and a broadcast behavior with spawning happening around March and May (Pires et al. 1999). In this pattern, gametic fertilization occurs in the water column, and the larva is exposed to dispersion by marine currents for more time. Consequently, this reproductive pattern is known for its wide dispersion and connectivity among populations (Veron 1995), although it does not always occur (Ayre and Hughes 2000, Miller and Ayre 2008). Then, this reproductive behavior could also be an alternative explanation to the few structure observer for *M. braziliensis.*

The two groups indicated by BAPS for *MaSC-1,* found with a low difference between then, could indicate the presence of two distinct areas that remained isolated for a short time and from where our sampled banks received immigrants. This disruption probably occurred before the LGM because the Paleoclimatic model (Figure 1) does not indicate the existence of two isolated refugia. Since these groups occur sympatrically and have no geographic correspondence, it is difficult to estimate the possible location of these previous refugia.

Phylogenetic inference and divergence time

The absence of different lineages within *Mussismilia braziliensis* highlights the low genetic structure in this group. Values of divergence time between this species and the outgroup along the Oligocene-Miocene evidenced by both markers (Figure 7) agree with their phylogenetic distance, since we are dealing with different genera. Further studies should include a closer group to estimate a more precise time of emergence for this specie. Concerning the time of diversification estimated during the Mio-Pliocene (Figure 7), other studies also found similar results for closer groups of *Mussismilia*. Schwartz et al. (2012) revealed that all components of the live Caribbean ‘’Faviids’’, recently classified as a sister group of the genus *Mussismilia* (Schwartz et al. 2012), have a time of diversification close to that of our data,

occurring from 4.66 Mya (95% HPD = 3.01 - 7.06 Ma) to 8.21 Mya (95% HPD = 8.77-20.09 Ma).

According to Schwartz et al. (2012), environmental changes that occurred from the Miocene to Pliocene, such as total closure of the Isthmus of Panamá, the decrease in sea level depth, primary productivity and turbidity in water and an increase in salinity and temperature (Mcneill et al. 2001, Jain and Collins 2007), favored a turnover of coral fauna and probably led to the diversification of 'Faviids'. Klaus et al. (2011, 2012) suggest that these changes led to the substitution of more heterotrophic species with bigger polyps and large tentacles by a more autotrophic species with small polyps. The polyps with intermediary sizes (8 to 10 mm in diameter – Budd et al. 2012) and the relatively high resistance to sedimentation of *Mussismilia braziliensis* (Loiola et al. 2013) indicate that its emergence during the Mio-Pliocene is probable. Fossils of this species were not registered during this period. However, this absence of records may be due in part to its similarity to and misidentification with other Caribbean groups to which the species has traditionally been assigned (e.g. *Acanthastraea braziliensis* Verrill, 1868).

Demographic analysis

Our analysis did not find signals of demographic fluctuation or a bottleneck during the Pleistocene. Although the results indicated that the potential area for occupancy by this species has increased from LGM to the present day (Figure 1), it may be possible that its effective population size has not increased significantly. A previous study carried out with polychaets of the genus *Phragmatopoma,* a sessile organism as corals, shows that this species increased its population since 0.2 Ma rather than since the LGM, but further discussion was not provided by the author. Probably, Pleistocene glacial cycles affected this species long before the Last Glacial Maximum.

Conclusion

Coupling different techniques to study the evolutionary history of the endemic coral species *Mussismilia braziliensis* revealed interesting information. ENM predictions indicate that this species have its distribution area reduced during LGM, but maintained approximately the same latitudinal amplitude. Differently to what was

hypothesized, the spatial region of refugia does not include the Vitória-Trindade Seamount Chain, but regions to the north of Abrolhos Bank. The genetic data show low structure, and it was not possible to identify ancient lineages or more diverse regions. However, these results is consistent with the probable few changes in the latitudinal amplitude of occurrence over geological time. The inclusion of other ancient paleo scenarios in ENM analysis and the use of more advanced molecular techniques will certainly develop the understanding of this kind of study. The comprehension of the evolutionary history of coral species and their population behavior during glacial cycles has an important application in helping recent concerns about the influence of climate change on the future of coral reef ecosystems.

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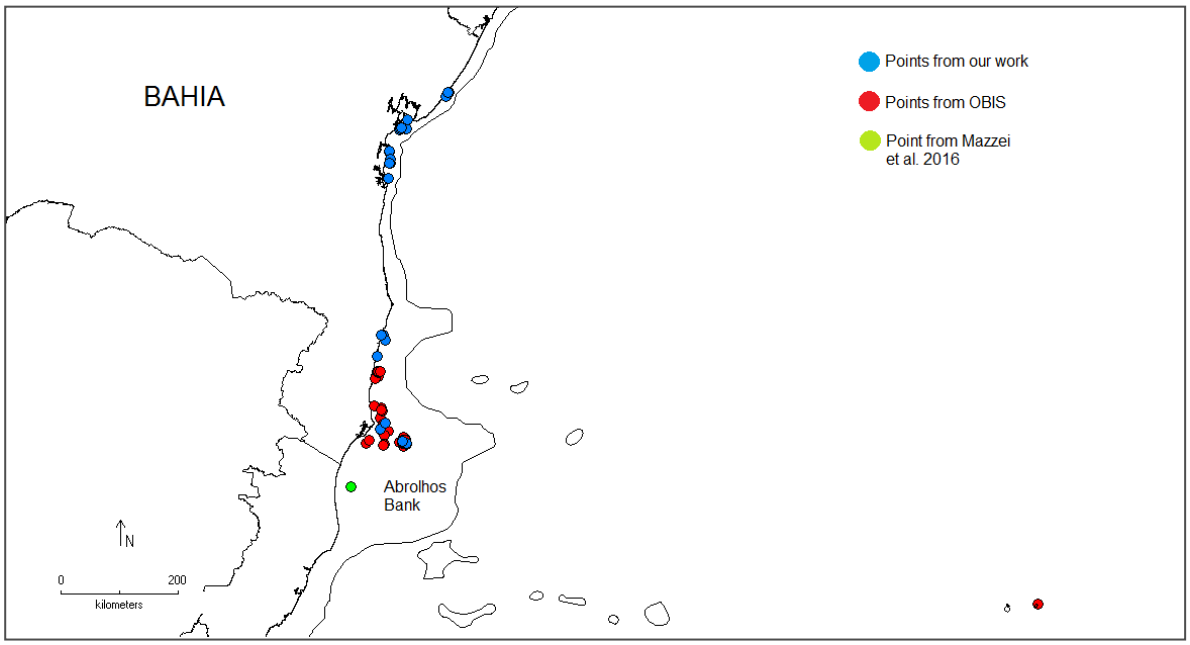
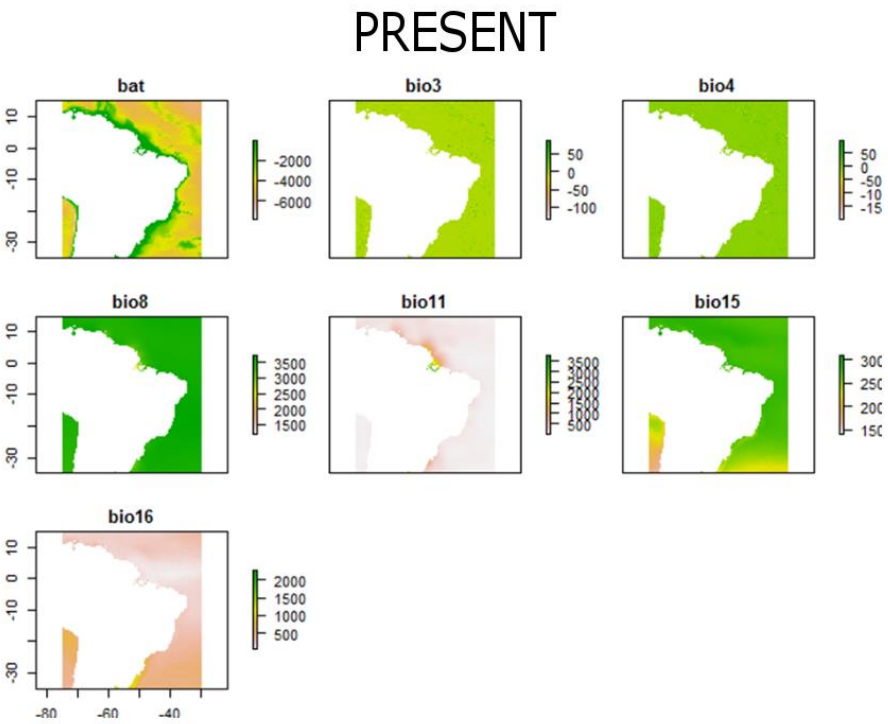
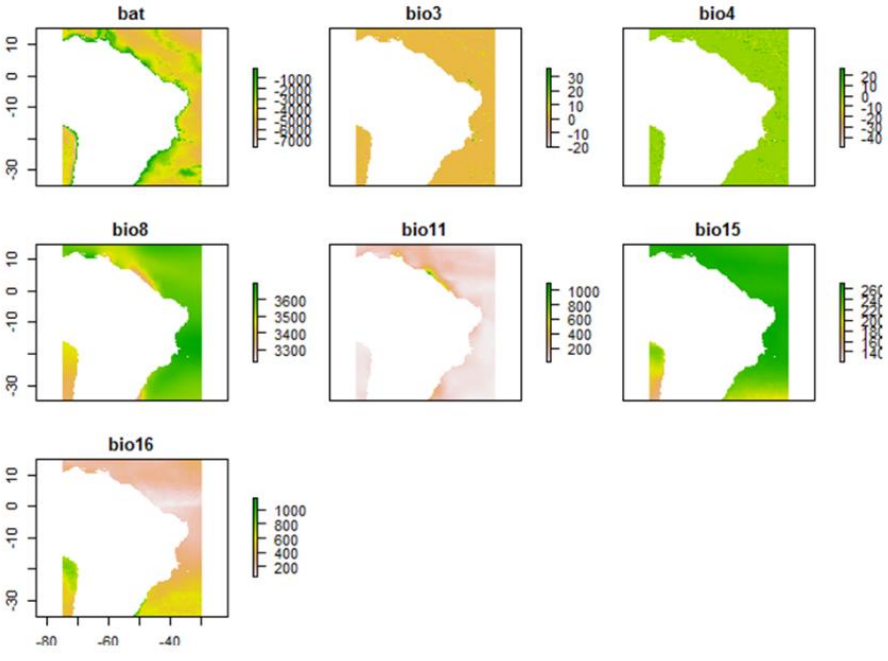
Supplementary information

Supplementary information 1. Distribution of points used to paleoclimatic modeling. Different colors indicates the data base from where points were collected.



Supplementary information 2. Layers from present and from Last Glacial Maximum used to ENM analysis. Bat = Bathymetry, Biogeo3 = Plan curvature, Biogeo4 = Profile curvature, Biogeo8 = Mean annual SSS (psu), Biogeo11 = Annual range in SSS (psu), Biogeo15 = SST of the warmest month (°C), Biogeo 16 = Annual range in SST (°C).





Supplementary information 3. Results of accuracy analisis ("thrs" “Auc” and “Tss”) from ENM of *Mussismilia braziliensis.*

BIOCLIN:

"AUC" "TSS"
"mbraziliensis1" 0.00116103 0.998012798438935 0.992424242424242
"mbraziliensis2" 0.00116103 0.999856519742883 0.996212121212121
"mbraziliensis3" 0.00115945 1 1
"mbraziliensis4" 0.00115945 0.996046491531282 0.988607558474479
"mbraziliensis5" 0.00116103 0.994318181818182 0.988636363636364
"mbraziliensis6" 0.00115945 0.999848772900104 0.996212121212121
"mbraziliensis7" 0.00494414 0.998063016528926 0.992424242424242
"mbraziliensis8" 0.00116103 1 1
"mbraziliensis9" 0.00116103 0.999849345730028 0.992424242424242
"mbraziliensis10" 0.00116103 0.999906737832874 0.996212121212121
"mbraziliensis11" 0.00116103 1 1
"mbraziliensis12" 0.00115945 0.994109344394515 0.984805277105657
"mbraziliensis13" 0.00115945 0.998098859315589 0.996197718631179
"mbraziliensis14" 0.00115945 0.996140108307409 0.988607558474479
"mbraziliensis15" 0.00116103 0.988492883379247 0.973484848484849
"mbraziliensis16" 0.00116103 0.996212121212121 0.992424242424242
"mbraziliensis17" 0.00116103 0.996212121212121 0.992424242424242
"mbraziliensis18" 0.00115945 0.998034047701348 0.9924098398433
"mbraziliensis19" 0.00116103 0.992044019742883 0.973484848484849
"mbraziliensis20" 0.00116103 0.998106060606061 0.996212121212121

GOWER:

"thrs" "AUC" "TSS"
"mbraziliensis1" 0.04519634 0.997905188246097 0.988636363636364
"mbraziliensis2" 0.04792018 0.999799127640037 0.988636363636364
"mbraziliensis3" 0.12478665 0.99994238967623 0.996212121212121
"mbraziliensis4" 0.12534081 0.999625532895495 0.988636363636364
"mbraziliensis5" 0.00998827 0.996169077134986 0.988636363636364
"mbraziliensis6" 0.04836348 0.999812766447747 0.992424242424242
"mbraziliensis7" 0.18963712 0.998019972451791 0.988636363636364
"mbraziliensis8" 0.04570076 1 1
"mbraziliensis9" 0.04539811 0.999770431588613 0.984848484848485
"mbraziliensis10" 0.04590252 0.999806301652893 0.984848484848485
"mbraziliensis11" 0.23555324 0.999928259871442 0.992424242424242
"mbraziliensis12" 0.00393023 0.999524714828897 0.988636363636364
"mbraziliensis13" 0.04609647 0.998098859315589 0.996197718631179
"mbraziliensis14" 0.40458514 0.997861216730038 0.981002995736836
"mbraziliensis15" 0.00473396 0.992079889807163 0.973484848484849
"mbraziliensis16" 0.04454061 0.998027146464647 0.992424242424242
"mbraziliensis17" 0.007214 0.997905188246097 0.988636363636364
"mbraziliensis18" 0.04508892 0.998005242539463 0.9924098398433

"mbraziliensis19" 0.04630605 0.999540863177227 0.981060606060606
"mbraziliensis20" 0.19224177 0.999885215794307 0.996212121212121

MAHALANOBIS DISTANCE:

"thrs" "AUC" "TSS"
"mbraziliensis1" -531.7225601 0.999928259871442 0.996212121212121
"mbraziliensis2" -24.73529131 0.999971303948577 0.996212121212121
"mbraziliensis3" -310.29564233 0.999971194838115 0.996212121212121
"mbraziliensis4" -37.68346414 0.999913584514345 0.992395437262358
"mbraziliensis5" -515.88622709 0.999942607897153 0.996212121212121
"mbraziliensis6" -16.93521875 1 1
"mbraziliensis7" -79.51551902 0.999942607897153 0.992424242424242
"mbraziliensis8" -178.64442806 1 1
"mbraziliensis9" -17.93913149 1 1
"mbraziliensis10" -81.4604323 0.999928259871442 0.992424242424242
"mbraziliensis11" -78.96134254 1 1
"mbraziliensis12" -451.8932715 0.999841571609632 0.988636363636364
"mbraziliensis13" -409.1617331 0.999971194838115 0.996212121212121
"mbraziliensis14" -23.16027289 0.999913584514345 0.992395437262358
"mbraziliensis15" -721.06207997 0.999727387511478 0.984848484848485
"mbraziliensis16" -399.00270271 1 1
"mbraziliensis17" -554.82575819 0.999942607897153 0.992424242424242
"mbraziliensis18" -356.69266907 0.999956792257172 0.996212121212121
"mbraziliensis19" -234.78952741 0.99974173553719 0.981060606060606
"mbraziliensis20" -172.52677939 0.999985651974288 0.996212121212121

MAXENT:

"thrs" "AUC" "TSS"
"mbraziliensis1" 0.13953881 0.999870867768595 0.992424242424242
"mbraziliensis2" 0.12046651 0.99982782369146 0.988636363636364
"mbraziliensis3" 0.27923979 0.999971194838115 0.996212121212121
"mbraziliensis4" 0.29784517 0.99982716902869 0.988636363636364
"mbraziliensis5" 0.15427654 0.999956955922865 0.996212121212121
"mbraziliensis6" 0.14565508 0.999913584514345 0.992424242424242
"mbraziliensis7" 0.47641416 0.99991391184573 0.992424242424242
"mbraziliensis8" 0.14222172 1 1
"mbraziliensis9" 0.13439813 0.999799127640037 0.981060606060606
"mbraziliensis10" 0.3817455 0.999813475665748 0.984848484848485
"mbraziliensis11" 0.32066466 0.999956955922865 0.996212121212121
"mbraziliensis12" 0.11372984 0.999409494181357 0.988636363636364
"mbraziliensis13" 0.17978071 0.999971194838115 0.996212121212121
"mbraziliensis14" 0.29884647 0.99982716902869 0.984848484848485
"mbraziliensis15" 0.08983454 0.999669995408632 0.981060606060606
"mbraziliensis16" 0.1370171 0.999985651974288 0.996212121212121
"mbraziliensis17" 0.12651266 0.999842171717172 0.992424242424242
"mbraziliensis18" 0.14769015 0.999956792257172 0.996212121212121
"mbraziliensis19" 0.4371769 0.999727387511478 0.984848484848485
"mbraziliensis20" 0.26950105 0.999842171717172 0.992424242424242

SVM:

"thrs" "AUC" "TSS"
"mbraziliensis1" 0.07645898 0.99110422405877 0.981060606060606
"mbraziliensis2" 0.19223104 0.999856519742883 0.988636363636364
"mbraziliensis3" 0.07182758 0.992784306947805 0.980988593155893
"mbraziliensis4" 0.43117132 0.996456965088144 0.988593155893536
"mbraziliensis5" 0.07060053 0.992825987144169 0.981060606060606
"mbraziliensis6" 0.07329922 0.998163670929831 0.984805277105657
"mbraziliensis7" 0.5782517 0.997403007346189 0.992424242424242
"mbraziliensis8" 0.67311189 1 1
"mbraziliensis9" 0.84742829 0.992510330578512 0.992424242424242
"mbraziliensis10" 0.0730455 0.994655360422406 0.981060606060606
"mbraziliensis11" 0.07294915 0.998242366850321 0.988636363636364
"mbraziliensis12" 0.16562407 0.999668740638322 0.984848484848485
"mbraziliensis13" 0.09155916 0.999985597419057 0.996197718631179
"mbraziliensis14" 0.39746485 0.996111303145524 0.984834082267542
"mbraziliensis15" 0.06389037 0.998593893480257 0.981060606060606
"mbraziliensis16" 0.28138316 0.989081152433425 0.984848484848485
"mbraziliensis17" 0.34373125 0.999038682277319 0.992424242424242
"mbraziliensis18" 0.12996425 0.99994238967623 0.9924098398433
"mbraziliensis19" 0.07035221 0.990881829660239 0.973484848484849
"mbraziliensis20" 0.303383 0.996470385674931 0.988636363636364

DISCUSSÃO GERAL

Diversidade, inferência filogenética e tempos de divergência do "Complexo *Siderastrea"* e da espécie endêmica *Mussismilia braziliensis.*

Este trabalho trouxe informações importantes sobre a diversidade e história evolutiva de dois grupos de corais que estão entre os principais construtores dos recifes brasileiros. As espécies do gênero *Siderastrea* e a *Mussismilia braziliensis* apresentaram diversidade haplotípica alta e diversidade nucleotídica baixa, um padrão comum encontrado para outras espécies de coral (Nunes et al. 2011, Nunes et al. 2009). Destaca-se que este trabalho fornece os primeiros dados sobre a diversidade genética de *M. braziliensis*, que apesar de ser uma espécie endêmica e de distribuição restrita, é ainda pouco estudada. Em relação ao gênero *Siderastrea*, as análises indicam que os indivíduos brasileiros são muito semelhantes geneticamente às espécies do caribe *S. radians* e *S. siderea* e que a espécie *S. stellata*, considerada endêmica para o Brasil (Leão et al. 2003), pode constituir em uma variação morfológica da espécie *S. siderea*. Estes resultados chamam a atenção para a necessidade de uma revisão do gênero considerando a proximidade filogenética entre *S. stellata* e *S. siderea* e não entre *S. stellata* e *S. radians*, como havia sido sugerido por outros trabalhos (Forsman et al. 2005), e a necessidade de se realizar análises comparativas genéticas e morfológicas considerando uma ampla amostragem no Oceano Atlântico.

Os resultados de tempo de divergência mostraram que os períodos de diversificação observados coincidem com períodos de grandes mudanças ambientais no Oceano Atlântico. A divergência de ~29.02 Ma apontada entre *S. radians* e *S. siderea* pode estar relacionada à intensificação das correntes e diminuição da temperatura da água no Atlântico Central entre o Oligoceno/Mioceno devido ao fechamento da conexão entre o Mar de Tethys e o Atlântico, à abertura do canal de Drake no Oceano Antártico (Smart and Murray 1994, Edinger and Risk 1995, Nisancioglu 2003) e à variações do nível do mar no período (Rossetti et al. 2013). Já, a diversificação de *M. braziliensis* entre o final do Mioceno e o início do Plioceno pode estar relacionada a diminuição do nível do mar, redução da produtividade e da turbidez da água e ao aumento da temperatura e salinidade na região (Mcneill et al. 2001, Jain and Collins 2007). De acordo com Schwartz et al.

(2012), este período foi de grande importância para diversificação de outros grupos da Família Faviidae a qual *M. braziliensis* pertence. Certamente, mais estudos são necessários para apoiar estas hipóteses, entretanto, as análises realizadas representam um passo importante para o entendimento da história evolutiva destes grupos.

Processos históricos responsáveis pela diversidade de corais na costa do Brasil

Embora as espécies do gênero *Siderastrea* e a espécie *M. braziliensis* possuam características biológicas e distribuições geográficas bastante diferentes, os resultados indicaram respostas semelhantes às variações ambientais ao longo do tempo geológico na costa do Brasil. As análises de diversidade genética, inferência filogenética e demografia não mostraram os sinais de colonização recente a partir do Caribe como foi proposto por Leão et al. (2003), e nem a partir de refúgios pleistocênicos em regiões de cadeias montanhosas próximas ao banco de abrolhos como sugerido por (Leão 1983); também não mostram expansão recente, indicando que as populações podem ter resistido a variações no nível do mar no Pleistoceno e mantido a sua amplitude de distribuição latitudinal. A simulação paleoclimática baseada em modelagem de nicho realizada para *M. braziliensis* também apontou para a manutenção na extensão latitudinal ocupada por essa espécie ao longo da costa durante o último máximo glacial.

Este resultado sugere que a costa do Brasil pode ter permanecido relativamente estável ao longo do tempo geológico em relação a outras regiões no Atlântico e, apesar de ser uma região marginal, mantido condições para o desenvolvimento de recifes. A discussão sobre a presença de uma fauna arcaica com características do terciário representada principalmente pelo gênero endêmico *Mussismilia*, que foi amplamente distribuído no Oceano Atlântico no passado, sugere que esta região seja uma área de sobrevivência para este gênero provavelmente devido a essa estabilidade (Leão 1983, Leão and Kikuchi 2005, Nunes et al. 2008). Trabalhos na literatura mostram que o Caribe sofreu grandes modificações geotectônicas como o fechamento do Istmo do Panamá e modificações na circulação (Edinger and Risk 1995, Nisancioglu 2003, O'Dea et al. 2016). Depósitos paleontológicos de recifes fósseis nesta região registram períodos de grandes

extinções seguidas de diversificações associados a esses eventos (Budd 2000a). Embora os dados obtidos tenham apontado para um cenário de maior estabilidade ambiental no Brasil, mais investigações são necessárias para avaliar a sua abrangência para a fauna de corais construtores brasileiros como um todo.

Outro padrão biogeográfico que foi aqui corroborado é a barreira na região entre 8 e 10º de latitude, encontrada para o gênero *Siderastrea*. Esta quebra já havia sido encontrada para este grupo em um trabalho com isoenzimas (Neves et al. 2008), e para outros grupos marinhos (Souza et al. 2017, Picciani et al. 2017). Em geral, tem sido atribuído ao desague do rio São Francisco e ao giro subtropical do Atlântico Sul que chega ao Brasil nessa região e bifurca para o sul formando a Corrente do Brasil e para o norte formando a Corrente Norte do Brasil (Carvalho and Kikuchi 2013). É uma quebra que provavelmente não foi responsável pela origem de *S. radians* e *S. siderea* uma vez que as espécies provavelmente divergiram muito antes, como mostrado pelas análises de tempo de divergência, entretanto, limita sua distribuição e sugere uma diferenciação de nicho entre elas. A espécie *M. braziliensis* parece também estar sujeita a essa barreira uma vez que ela aparentemente restringe a sua distribuição a norte. Contudo, esta espécie parece também estar limitada a sul por uma quebra na região do Rio Doce, também observada para outras espécies (Picciani et al. 2017). A presença dessas quebras reforça a ideia de que a região de ocorrência de recifes na costa brasileira não é uma única unidade biogeográfica. Como indicado por Leão et al. (2003), ela apresenta quebras que precisam ser consideradas em futuros trabalhos filogenéticos e filogeográficos.

Por fim, destaca-se o a importância deste trabalho em tentar entender os processos biogeográficos históricos responsáveis pela distribuição da biodiversidade atual de corais escleractíneos da costa do Brasil. Trata-se também de um trabalho pioneiro por associar abordagens filogeográficas baseadas em análises de coalescência e simulações paleoclimáticas baseadas em modelagem de nicho para acessar estes processos.

CONCLUSÕES GERAIS

- As análises filogeográficas para os dois grupos estudados, o gênero *Siderastrea* e a espécie *Mussimsilia braziliensis,* não mostraram sinais de colonização recente a partir do Caribe ou a partir de refúgios pleistocênicos em regiões de cadeias montanhosas próximas ao Banco de Abrolhos, indicando que elas podem ter resistido a variações no nível do mar desde o Último Máximo Glacial e mantido a sua amplitude de distribuição latitudinal até o presente.

- Os resultados de tempo de divergência indicaram que mudanças ambientais que ocorreram entre o Oligoceno/Mioceno e entre o Mioceno/Plioceno foram importantes para a diversificação dos grupos estudados.

- Os dados obtidos apoiam a presença de uma barreira biogeográfica na região entre as latitudes 8 e 10º, padrão que tem sido discutido na literatura.

- A associação entre análises filogenéticas e morfológicas do gênero *Siderastrea* indicaram a necessidade de realização de uma revisão taxonômica do grupo, levando em consideração a proximidade entre *S. siderea* e *S. stellata* e a uma ampla amostragem no Oceano Atlântico.

- As simulações paleoclimáticas para a espécie *M. braziliensis* apoiaram os resultados obtidos pelos dados genéticos uma vez que indicaram que embora a distribuição potencial desta espécie tenha reduzido no Último Máximo Glacial, a sua amplitude latitudinal de ocorrência se manteve.

- A integração de diferentes metodologias, análises filogeográficas, informações morfológicas e modelagem de distribuição, se mostrou uma boa abordagem para estudar os processos históricos responsáveis pela distribuição da biodiversidade de corais escleractíneos na costa brasileira.

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ANEXOS

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DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada ***"FILOGEOGRAFIA DE CORAIS ESCLERACTÍNEOS ZOOXANTELADOS (CNIDARIA: SLERACTINIA) DA COSTA DO BRASIL"***, desenvolvida no Programa de Pós-Graduação em Biociências e Tecnologia de Produtos Bioativos do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

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